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Factors that drive demographic change in a community of albatrosses

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Declaration of Originality

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Abstract

Understanding the ecological relationships between a species and the environment it inhabits is critical to determining species resilience to environmental change and future population viability. By assessing ecological relationships across multiple species greater insights into species intrinsic adaptations and external environmental factors can be revealed, contributing to a broader understanding of community ecology.

This thesis examines the foraging behaviours and environmental drivers of demographic variability of four albatross species from subantarctic Macquarie Island (black-browed *Thalassarche melanophris*, grey-headed *T. chrystostoma*, light-mantled *Phoebetria palpebrata* and wandering albatrosses *Diomedea exulans*) to understand the ecological, morphological and life history relationships that influence species resilience to ecological shifts.

Three of the four albatross species that inhabit Macquarie Island exist in small populations of less than 80 breeding pairs (for light-mantled albatross the current breeding population estimate is approximately 2 150 pairs). Consistent monitoring since 1994 shows varied population trends among the species; black-browed and light-mantled albatrosses are increasing, while the grey-headed albatross population remains stable and the wandering albatross population is declining. The decline of Macquarie Island's wandering albatrosses is attributed to long-line fishing operations, however for the remaining species, population and demographic drivers are unidentified. Aside from the threat to survival presented by fisheries, Macquarie Island albatrosses face climate-driven changes to physical oceanic processes including a southerly shift in frontal positions, intensifying wind patterns and greater variability in sea ice dynamics. For albatrosses, such changes are predicted to alter the structuring of prey resources and influence the energetic costs of foraging, ultimately compromising their capacity to survive and reproduce. At the colony, trends in the reproductive output of Macquarie Island albatrosses may be influenced by severe habitat degradation, including vegetation suppression and landslides, caused by the grazing of invasive rabbits.

Specifically, this thesis aims to: 1) identify important at-sea habitats and vulnerability to climate change in the Southern Ocean 2) understand the indirect impacts of onshore change

caused by climate change and invasive species on albatross reproductive output 3) quantify the relative contribution of at-sea (climate change and fisheries) and onshore change (habitat degradation and weather) to demographic variability.

1) Habitat models of residence time from tracking data of all four species (n = 47, 1994-2009) were used to quantify the physical features associated with core foraging areas. During the breeding season, species overlap was high close to the island, extending north into the Tasman Sea. Conversely, nonbreeding albatrosses showed high variability in habitat use across wide ocean expanses but similarly used productive frontal regions and associated mesoscale eddies. Residence times were linked to moderate wind speeds for all species, suggesting that birds use areas where the aerodynamic performance will be greatest, reflecting morphological adaptations. Given the core foraging areas identified, and the functional and life history adaptations of each species, it is expected that of the four albatross species breeding on Macquarie Island, black-browed albatross may be more vulnerable to future climate-driven changes to wind patterns in the Southern Ocean and potential latitudinal shifts in the Subantarctic Front;

2) To quantify the influence of invasive European rabbits *Oryctolagus cuniculus* and extreme weather patterns on the reproductive output of three escarpment nesting albatross species (black-browed, grey-headed, and light-mantled albatrosses) demographic multi-event models were applied to 20 years of mark-recapture data. High rabbit densities corresponded to reduced breeding propensity of all species, with severe declines observed during periods of highest rabbit numbers. For one species; the black-browed albatross, the combination of extreme rainfall and high rabbit density significantly explained reduced breeding success. These results show the cascading and compounding effects of a successful mammalian invader and extreme weather events on the reproductive output of a community of albatross species, offering compelling support for active management of island ecosystems;

3) The temporal variability in survival, breeding propensity and success was assessed using 20 years of mark-recapture data from four species of Macquarie Island albatrosses. For three species (excluding wandering albatrosses), the influence of oceanic, fisheries and onshore change were investigated using multi-event models to

give insight into future population viability. Large-scale climate cycles; the Southern Annular Mode and the El Niño/Southern Oscillation explained significant variability in the survival of all species. For black-browed albatrosses, south-west Atlantic longline and New Zealand trawl fisheries effort described variability in survival. These findings suggest that managing drivers of negative demographic trends that may be more easily controlled, such as fisheries and habitat degradation, will be a viable option for some species (e.g. black-browed albatrosses) but less effective for others (e.g. light-mantled albatrosses), as opposed to drivers which are not easily mitigated, such as climate change. These findings illustrate the importance of integrating oceanic, fisheries and onshore threatening processes when assessing demographic variability and the development of management policy;

The results of this study suggest that managing sources of negative demographic trends that are more easily controlled, such as fisheries and habitat degradation, as opposed to those which are not; such as climate change, may be a viable option for some species (e.g. black-browed albatross) and less effective for others (e.g. light-mantled albatross). Subsequently, this study provides support for evidence-based conservation planning for these populations as well reduces outcome uncertainty of future management actions for other marine predator populations. Furthermore, this study has provided new insights into the ecology of a community of Southern Ocean predators and has broader applications for understanding the responses of multiple sympatric species to multiple environmental stressors.

Statement of Publication & Co-authorship

Chapters 2, 3 and 4 in this thesis are manuscripts in review or in preparation for submission to a peer reviewed journal.

The following people and institutions contributed to the publication of the work undertaken as part of this thesis:

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Chapter 2: Functional morphology and life history influence habitat use of an albatross community

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Co-author contributions:
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Chapter 3: Introduced rabbits and extreme weather events: a dangerous combination for the reproductive output of three sympatric albatrosses

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Chapter 4: Deconstructing the influence of three major threat types on the demography of an albatross community

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Table of Contents

Chapter 1

General Introduction

Global climate change is rapidly transforming ecological processes in the marine environment (Hoegh-Guldberg and Bruno, 2010). The Southern Ocean is an important component in the earth's ocean and climate system and is currently showing evidence of unprecedented shifts in oceanographic processes such as changes in frontal positions (Sokolov and Rintoul, 2009), wind patterns (Marshall, 2003) and sea ice dynamics (Stammerjohn et al., 2012). Climate-driven changes in the Southern Ocean are not occurring in isolation but simultaneously with evolving fisheries, and in the terrestrial realm, with the proliferation of invasive species, which represent multiple stressors that can influence populations, communities and ecosystem structure (Clarke and Harris, 2003, Tuck et al., 2003). The high trophic position of marine predators sees that they respond to bottom-up processes that permeate through lower trophic levels and directly influence prey resources. Bottom-up stressors that influence foraging efficiency may ultimately be reflected at the population level because demographic parameters are affected by the allocation of energetic resources to individuals (Frederiksen et al., 2006). Similarly, artificial top-down stressors, such as that caused by fisheries, that can reduce survival may translate into a population decline and even result in trophic cascades (Baum and Worm, 2009). Understanding how marine predator populations respond to changes in their environment also provides insight into the physical processes that affect prey availability and the severity of top-down threats, and ultimately supports the prediction of long-term population viability. Biotelemetry and long-term mark-recapture studies offer mechanisms to investigate the links between ecological change, foraging ecology and demographic processes (Besbeas et al., 2002, Cooke et al., 2004). Furthermore, studies that integrate multiple species provide greater insight into adaptive capacity and the extent of threats to the ocean system. This is because, within a community, different species have different morphology and life history adaptations that influence the trade-off between survival and reproduction and plasticity to change.

Southern Ocean albatrosses

Albatrosses spend most of their lives traversing the open ocean, only returning to land to breed. They are highly philopatric, breeding at natal colonies once reaching maturity between

4-16 years on average (Warham, 1990). Following recruitment, breeding occurs either annually or biennially for most species (Jouventin and Dobson, 2002). However, these breeding regimes are not fixed and show variation among individuals and populations. Adults invest considerable energetic resources in egg development and chick growth, which progresses slowly and, if successful, results in a single high-quality offspring (Weimerskirch et al., 2000a, Shaffer, 2004). Adult survival is naturally high, with individuals of some species living up to 50 years (Weimerskirch et al., 1987). These life history traits characterise albatrosses as classic K-selected taxa. As long-lived species, albatrosses have many opportunities to breed and can miss some breeding opportunities with little consequence for individual fitness and lifetime reproductive output.

Albatrosses are characterised by their immense wingspan that enables efficient long distance excursions to productive regions (Spear and Ainley, 1997a). In flight, their wing morphology creates great lift and little drag contributing to their superior aerodynamic performance (Warham, 1977, Pennycuick, 2008, Suryan et al., 2008). Furthermore, albatrosses gain kinetic energy in flight through dynamic soaring by exploiting the wind shear between wave troughs and the prevailing wind to range widely at relatively low energetic cost (Wilson, 1975, Sachs et al., 2012). During the breeding season, they are central place foragers, returning regularly to the colony for incubation and chick-rearing (Pinaud and Weimerskirch, 2005). When released from the cost of breeding, albatrosses exhibit free ranging behaviour, confined only to regions where wind conditions enable efficient flight (Suryan et al., 2008). For some species, the unobstructed circumpolar winds of the Southern Ocean support circumpolar navigations (Weimerskirch et al., 2014, Clay et al., 2016). With morphology and life history traits that enable wide-ranging foraging, albatrosses exhibit flexibility suited to highly dynamic environments like the Southern Ocean, where prey resources are patchy and vary through space and time. The combination of long-range pelagic foraging behavior of albatrosses and the highly dynamic environment they inhabit limits our ability to quantify the effects of environmental state.

Albatrosses face numerous threats at sea and on land (Croxall et al., 2012, Phillips et al., 2016). Rapid and widespread population declines of several species have been attributed to incidental bycatch in longline and trawl fisheries (Gales and Robertson, 1998, Dunn et al., 2007, Phillips et al., 2016). Mortality can occur as albatross dive to take baited hooks or through entanglements or collisions with fishing gear (Furness, 2003, Anderson et al., 2011).

Over the last decade, policy implementation and technological advances in bycatch mitigation, such as the use of exclusion devices (Maree et al., 2014), integrated lines (Robertson et al., 2010) or underwater setters (Gilman et al., 2003) have resulted in population stability and minor increases in a small number of colonies (Inchausti and Weimerskirch, 2001, Robertson et al., 2014). However, as albatross distributions often span multiple regional, national and international fisheries management boundaries, considerable variation exists in the application of mitigation measures (Cooper et al., 2006).

Closely tied to the negative effects of fisheries bycatch is the influence of fisheries discards on albatross survival. Over generations, albatrosses have learned to associate fisheries vessels with a profitable secondary food resource (Granadeiro et al., 2011). The scavenging of offal discharged from vessels can have a positive and indirect effect on demographic traits by improving energetic resources and subsequently boosting survival and/or reproductive output (Rolland et al., 2008). Discarding practices also vary widely across different fisheries and countries, which have varied regulatory measures in place to limit interactions between fishing vessels and seabirds (AFMA, 2013, Votier et al., 2004, Furness et al., 2007).

At the colony, albatrosses face pressures that can affect reproduction and survival, including habitat change, the threat of invasive species and disease. Amongst invasive species, introduced mammals are particularly problematic for seabirds and can transform island ecosystem dynamics through predation (Cuthbert and Hilton, 2004), competition for habitat (Brothers and Bone, 2008) or habitat degradation (Weimerskirch et al., 1989). Invasive rodents and cats are known predators of albatross adults, chicks and eggs. However the demographic consequences of habitat competition and degradation are less clear (Wanless et al., 2009, Phillips et al., 2016). As islands often represent breeding habitat for many seabird species, changes in habitat quality or the influence of invasive species can have a profound effect on a whole community of seabird species simultaneously. Another emerging and growing threat at albatross breeding colonies is infectious disease, however little is known about its incidence or prevalence, particularly in synergy with changing environmental conditions driven by global climate change (Weimerskirch, 2004).

The influence of global climate change can affect albatross populations through an array of mechanisms. Climate-driven changes in ocean circulation and upwelling processes that structure primary productivity can regulate albatross prey resources. Alternatively, changes

can influence the energetic cost of flight or thermoregulation during incubation or chick growth through changes in wind patterns (Weimerskirch et al., 2012) and local weather at the colony (Thomson et al., 2015). The pervasive influence of climate change on oceanic and onshore processes means the full extent of its ecological consequences for albatrosses are not well understood. Furthermore, the synergistic effect of multiple stressors such as fisheries, invasive species and climate change may be amplified or dampened by the life history traits of albatrosses. The combination of low fecundity, slow life cycle and high survival rates suggest that any artificial increase in mortality or prolonged decreases in reproductive output has important consequences for population viability, even if these might take some time to become visible in the population (Phillips et al., 2016).

Understanding the environmental relationships that influence the foraging behaviours and demographic variability of albatrosses is central to determining their resilience to environmental change and population viability. By assessing ecological relationships across multiple albatross species, greater insights into intrinsic species adaptations and external environmental factors can be revealed, contributing to a broader understanding of community ecology. Furthermore, understanding the relative influence of the main threats on albatross demographic parameters supports evidence-based conservation planning.

Study species and site

Subantarctic Macquarie Island (54.6° S, 158.9° E) is a narrow, elongated island situated on the Macquarie Ridge in the south-west Pacific sector of the Southern Ocean (Fig. 1). The coastal perimeter of the island, steep escarpment and central plateau provide breeding habitat for vast congregations of wildlife, including penguins, seabirds and seals. Nearby, the Subantarctic Front interacts with the Macquarie Ridge, a region of steep bathymetry, generating strong upwelling and supporting higher surface productivity and prey resources for higher trophic predators (Robinson et al., 2002, Terauds et al., 2006a, Sokolov and Rintoul, 2007, Flynn and Williams, 2012).

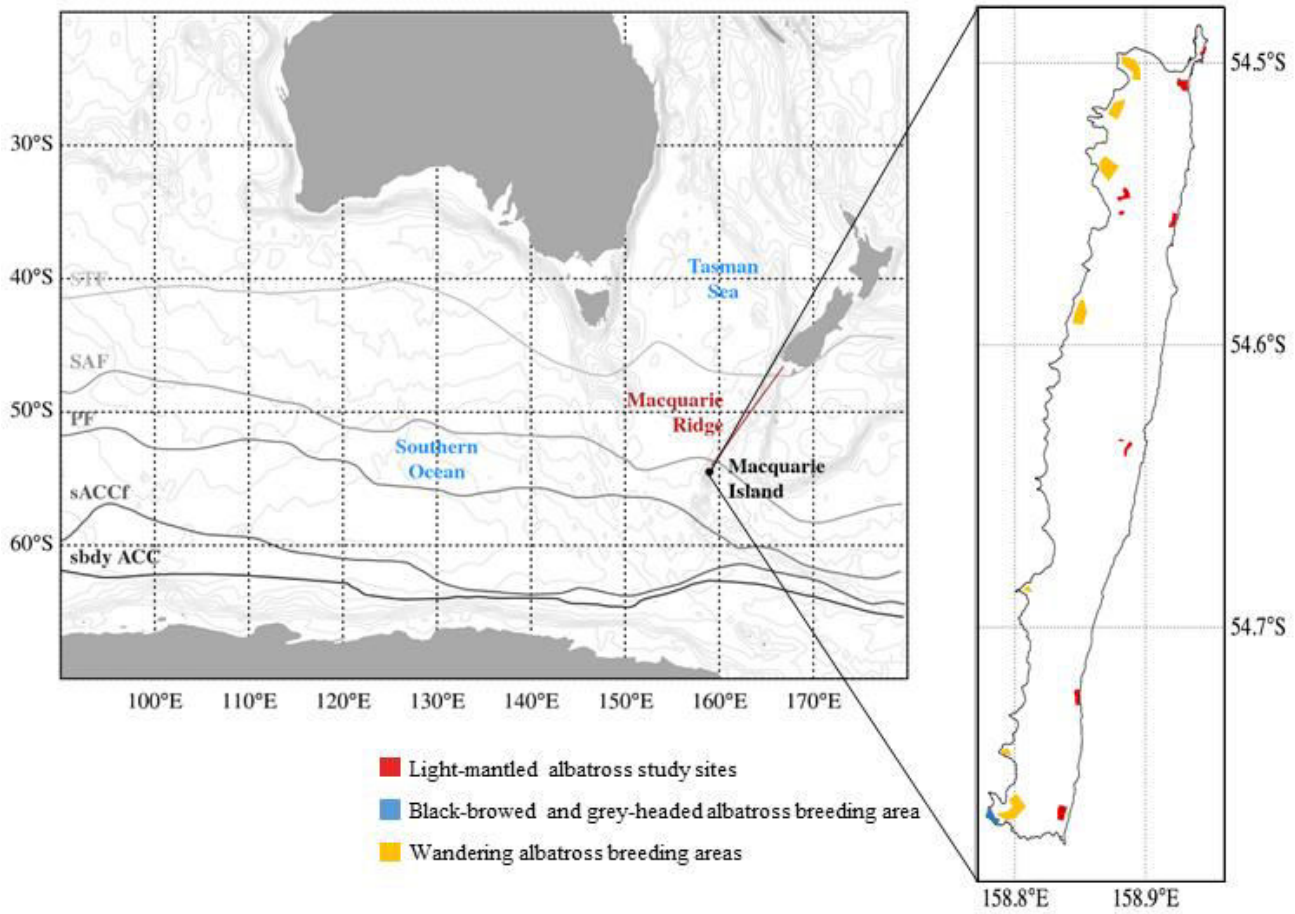

Figure 1 Subantarctic Macquarie Island in relation to major Southern Ocean frontal systems; Subtropical Front (STF), Subantarctic Front (SAF), Antarctic Polar Front (PF), Southern Antarctic Circumpolar Front (sACCf) and the southern boundary of the Antarctic Circumpolar Current (sbdy ACC). Inset: Albatross breeding areas and study sites at Macquarie Island.

Macquarie Island is a nationally important breeding site for four species of albatrosses, black-browed *Thalassarche melanophris*, grey-headed *T. chrysostoma*, light-mantled *Phoebetria palpebrata* and wandering *Diomedea exulans*, representing three of the four genera of the albatross family. The populations within this community have differing long-term trends; two species are listed as near threatened and are increasing in size (black-browed and light-mantled albatrosses), one is listed as vulnerable and decreasing (wandering albatross) and one is endangered with a stable population trajectory (grey-headed albatross) (Fig. 3, Chapter 4) (DPIPWE, 2011, IUCN, 2017). Furthermore, these species are separated by morphology, phenology and life history traits. Most evident are differences in wing structure and body size, ranging from the smaller light-mantled albatrosses, which possess shorter narrower wings, to the larger wandering albatrosses, which has the greatest wingspan and wing area. The breeding phenology of the annual breeding black-browed albatrosses and the biennial breeding grey-headed, light-mantled and wandering albatrosses is also offset and have varying incubation and chick-rearing durations (Fig. 2). Except for light-mantled albatrosses, these populations are small (less than 80 breeding pairs), increasing their risk of local extinction and making the community a priority for conservation. Declines in wandering albatross survival have previously been linked to bycatch in tuna longline fisheries (de la Mare and Kerry, 1994, Terauds et al., 2006b), although no such links have been established for black-browed or grey-headed albatrosses (Terauds et al., 2005) and for light-mantled albatrosses no assessment exists.

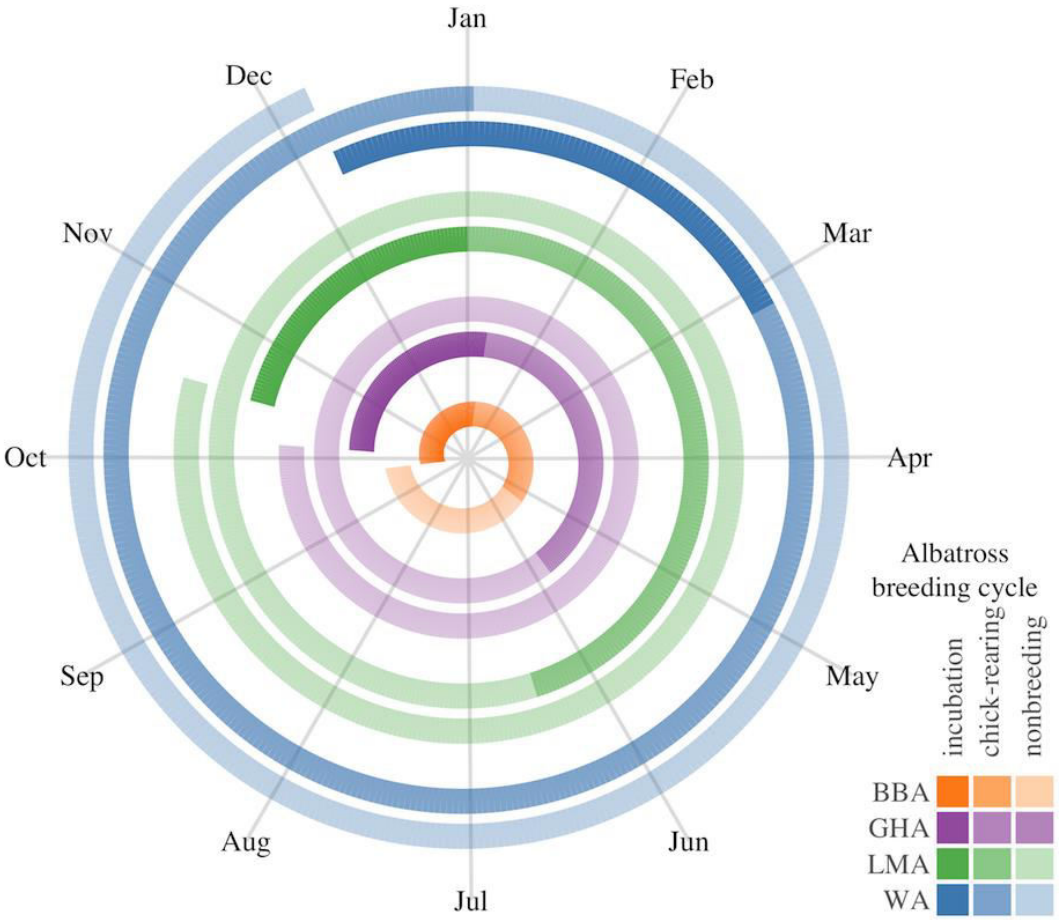

Figure 2 Multi-year breeding cycles of black-browed (BBA), grey-headed (GHA), light-mantled (LMA) and wandering albatrosses (WA) at Macquarie Island (adapted from Terauds, 2002).

Subantarctic Macquarie Island has experienced drastic change over the last ~140 years due to the establishment and proliferation of invasive species. First introduced by pre-industrial commercial sealers in the late 19th century; cats *Felis catus*, weka *Gallirallus australis scotti*, rabbits, rats *Rattus rattus* and mice *Mus musculus* have had considerable negative consequences for the island's ecology. Before they were eradicated in 2000, feral cats preyed heavily on rabbits and burrowing petrels, using both as a primary prey source (Jones, 1977, Brothers and Bone, 2008). However, there are no indications that cats regularly preyed upon nesting albatrosses, possibly due to the high availability of alternative prey and an effective defence mechanism: the regurgitation of stomach oil (Jones, 1977). Furthermore there is no evidence to suggest that Weka depredated albatross eggs on Macquarie Island, despite this occurring on Solander Island and the Chatham Islands in New Zealand (Taylor, 2000, Miskelly et al., 2008). Rats and mice depredate burrowing petrel eggs and chicks, and rabbits caused severe vegetation suppression and enhanced slope erosion. During the 2000s the

coastal escarpment of Macquarie Island experienced catastrophic degradation due to high rabbit densities. Especially serious was the slope degradation at the southern end of the island, where black-browed and grey-headed albatrosses nest. In 2014, one of the largest and most ambitious invasive species eradications to date was deemed successful in removing these three species from Macquarie Island (Springer, 2016). The success of the Macquarie Island Pest Eradication Project in removing invasive vertebrates from the island has resulted in rapid vegetation recovery and increases in burrowing petrel occupancy (Shaw et al., 2011, Springer, 2016). The effect of deterioration and subsequent recovery of albatross nesting habitat has unknown consequences for reproductive behaviours of these populations.

Over the last four decades, the island has also experienced increases in surface air temperatures, total annual precipitation and wind speeds attributed to global climate change (Adams, 2009, Hindell et al., 2012, Hande et al., 2012). Recent changes in the local climate have consequences for endangered native flora (Bergstrom et al., 2015). However, the implications for seabirds are yet to be determined.

The waters surrounding Macquarie Island that are in the Australian Economic Exclusion Zone are subject to commercial trawl and longline fishing for Patagonian Toothfish *Dissostichus eleginoides* by one or two vessels every year (AFMA, 2006). Seabird bycatch in the Macquarie Island Toothfish Fishery is heavily mitigated, and as a result, there have been no albatross deaths since operations commenced in 1994 (AFMA, 2013). Furthermore, a Commonwealth Marine Reserve exists to the south-east of Macquarie Island and represents one of the world's largest 'no take' areas (sanctuary zone) where commercial fishing is prohibited (Fig. 3) (AFMA, 2013). This region is of ecological significance for multiple higher order predators that breed on Macquarie Island including fur seals, elephant seals and penguins (Hull, 1997, Robinson et al., 2002, Wienecke and Robertson, 2002, Hindell et al., 2016). Furthermore, the habitat use of breeding black-browed and grey-headed albatrosses overlaps with the Macquarie Island Toothfish Fishery and the marine reserve, however, as wide-ranging species, their distribution extends beyond this to span multiple regional, national and international fisheries management boundaries (Terauds et al., 2006a). Understanding how individual fisheries influence the survival of albatross populations across their distribution is vital for informing management policy. However, for Macquarie Island albatrosses no spatially explicit analysis of fisheries impacts exists.

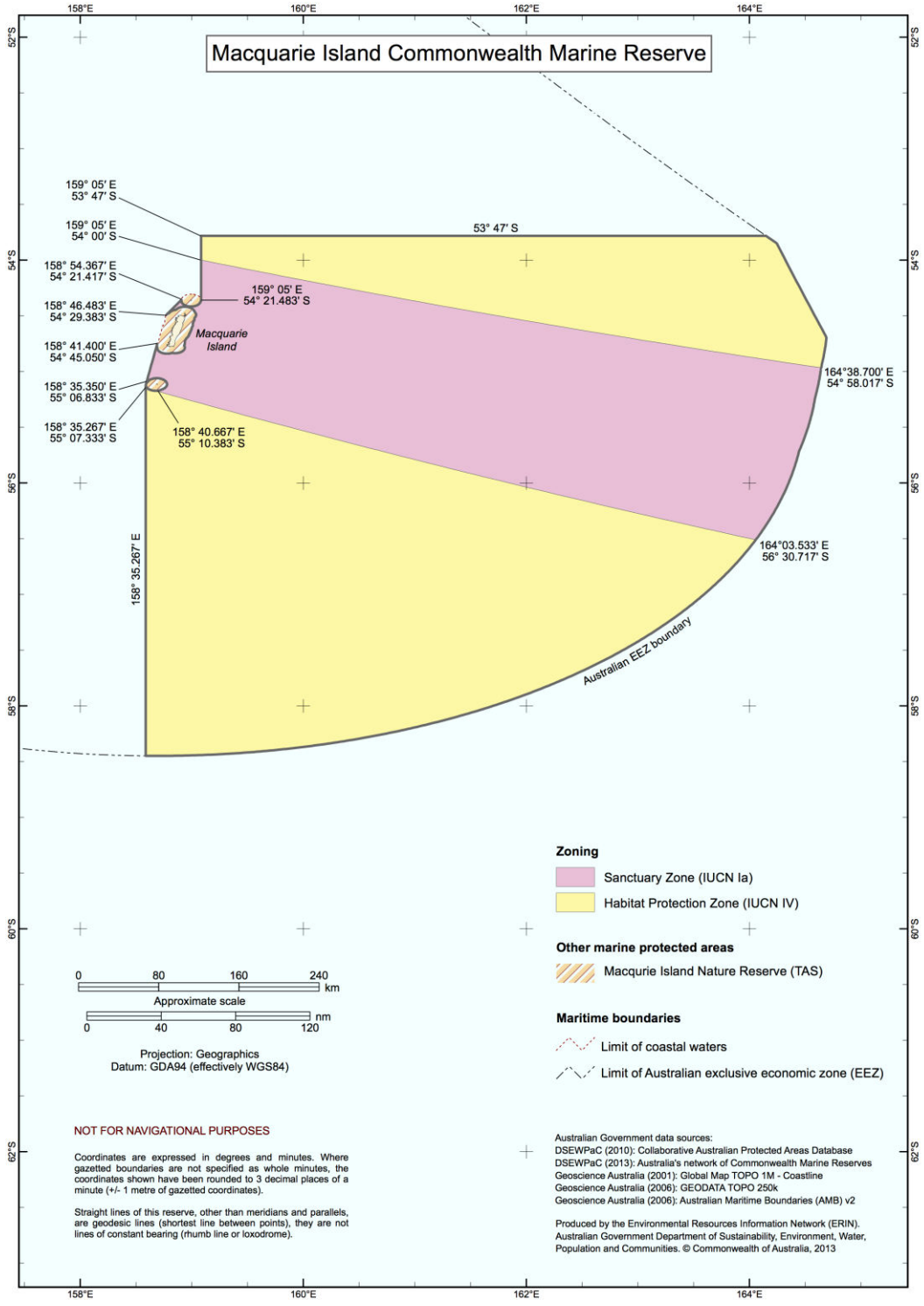

Figure 3 Map of the Macquarie Island Commonwealth Marine Reserve sourced from the Environmental Resources Information Network (ERIN), Department of Sustainability, Environment, Water, Population and Communities, 2013.

Study objectives

Information on the environmental drivers of foraging success and demographic rates of marine predators is central to informing management bodies. The overarching aim of this thesis was to quantify the ecological relationships that influence habitat use and demographic variability of a community of albatross species. The primary objectives of this research were achieved using historical tracking data and an extensive mark-recapture dataset spanning 20 years. The thesis is organised into three research chapters.

Chapter 2 – *Albatross community habitat use*

Using a multi-year tracking dataset, I aimed to determine the environmental features influencing at-sea habitat use of Macquarie Island albatrosses and understand how morphology and life history constraints affect foraging distribution and consequently, vulnerability or resilience to environmental variability.

Chapter 3 – *Onshore determinants of reproductive output*

To understand the importance of onshore factors on reproductive output I aimed to quantify the relationship between habitat degradation caused by invasive rabbits and extreme weather conditions on the breeding propensity and breeding success of three Macquarie Island albatross species. Understanding the influence of these factors will provide insights into population dynamics of albatross populations and provide a basis for assessing the implications of active management at colonies, such as the eradication of invasive species.

Chapter 4 – *Major threats influencing demographic variability*

Using a 20-year mark-recapture dataset, I aimed to determine the influence of fisheries, oceanic and onshore threats on the demography of the Macquarie Island albatross community by using fisheries and oceanographic covariates from the at-sea distribution of each Macquarie Island albatross species (Chapter 2) and the onshore drivers of reproductive output from Chapter 3.

Thesis structure

This thesis has been written as a series of self-contained manuscripts. Consequently, there is some overlap of text, conceptual figures and ideas between chapters. All chapters, except this introductory chapter and general discussion, consist of manuscripts that have been submitted to peer-reviewed journals or are in preparation for submission. The demographic data in

Chapter 3 and 4 required significant data quality control to ensure accuracy. The framework for database management performed in this thesis is contained in Appendix 1 and details of a science communication initiative related to this research in Appendix 2. I, Jaimie Cleeland, am the senior author of each paper. Co-authors are listed with each chapter title, and their contributions are detailed in the Statement of Co-authorship at the front of this thesis. A single bibliography is presented at the end of the thesis using the Harvard referencing style.

Chapter 2

Functional morphology and life history influence habitat use of an albatross community

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Abstract

Spatial segregation in habitat use of sympatric species is influenced by variability in functional morphology and life history trade-offs and is expected to shape species resilience to environmental change. To determine differences in year-round habitat use and gain insight into how morphological and life history traits influence foraging of an albatross community from subantarctic Macquarie Island (54.6° S, 158.9° E), I quantified the physical features associated with their core foraging areas based on habitat modelling of residence time of 10 black-browed, *Thalassarche melanophris*; 10 grey-headed, *T. chrysostoma*; 15 light-mantled, *Phoebetria palpebrata*; and 12 wandering albatrosses, *Diomedea exulans* tracked in 1994-2009. Overlap among the four species was high close to the island during the breeding season, extending north into the Tasman Sea. Nevertheless, black-browed albatrosses foraged more locally than the other species, perhaps attributable to a shorter breeding cycle, and morphological traits that incur greater flight costs. Nonbreeding albatrosses showed high variability in habitat use across wide ocean expanses, but all used highly productive frontal regions and mesoscale eddies. High residence times during the breeding and nonbreeding periods were associated with moderate wind speeds for all species (excluding breeding black-browed albatrosses), suggesting that birds use areas in which aerodynamic performance will be highest. Given the core foraging areas identified, and the functional and life history adaptations of each species, I suggest that black-browed albatross breeding on Macquarie Island will be more vulnerable to future climate-driven changes to wind patterns in the Southern Ocean, and potential latitudinal shifts in the Subantarctic Front.

Introduction

The functional morphology and life history traits of a species represent evolutionary trade-offs that determine the ability of individuals to exploit the environment to maximise energy acquisition and minimise expenditure. As oceanographic shifts drive changes in environmental structure across the distribution of an animal, its behavioural plasticity, influenced by functional morphology and life history traits, determine the extent to which it can adapt and successfully reproduce (Lescroël et al., 2010, Carneiro et al., 2015). Understanding the capacity of individuals and populations to respond to changes in the environment is critical, given the scale of recent and unprecedented ecosystem shifts driven by global climate change (Abadi et al., 2016, Descamps et al., 2016).

Variability in habitat use within a community of species reflects the diversity in functional morphology and life history adaptations (Costa, 1991, Zhang et al., 2007). The ability to use alternative habitats determines the vulnerability of each species to environmental changes and anthropogenic threats, providing essential information for evidence-based conservation planning (Waldron et al., 2006, McGowan et al., 2016). Community-level assessments of habitat use can also reveal areas of high ecological significance where the distributions of multiple species overlap. These may indicate regions of greater biodiversity and be candidate areas for protection (Raymond et al., 2015, Tancell et al., 2016, Thiers et al., 2016). Ultimately, determining the characteristics of the key foraging areas of a community of species allows better quantification of the links between environment, functional morphology, life history and population dynamics.

In the Southern Ocean, productivity is unevenly distributed in space and time; rather, it is concentrated in areas where available nutrients and light permit phytoplankton growth (Sullivan et al., 1993, Pakhomov and McQuaid, 1996, Moore and Abbott, 2000). For marine predators, macro- and mesoscale oceanographic features, such as frontal regions and eddy structures, are associated with greater predictability in resource distribution and act as prey-aggregating systems (Dragon et al., 2010, Bost et al., 2009, Scales et al., 2014). Nutrient retention and enrichment of surface waters through upwelling and mixing at frontal and mesoscale cyclonic eddy features can support higher phytoplankton concentrations relative to surrounding waters (Mitchell et al., 1991, Sokolov and Rintoul, 2007). As climate change continues to influence the oceanographic characteristics and productivity of the Southern Ocean (Sarmiento et al., 2004, Turner et al., 2014), understanding the constraints on distribution set by the morphological and life history traits of predators may help us to forecast climate-mediated futures for their populations (Constable et al., 2014).

Morphologically, albatrosses are adapted to fly efficiently over long distances. Their long narrow wings (high aspect ratio; the square of wingspan divided by the wing area) promote maximum flight efficiency by ensuring great aerodynamic lift and less induced drag, supporting long distance migrations (Pennycuick, 2008). Furthermore, the high body mass, long wingspan and large wing area of albatrosses allows them to achieve high glide ratios, gaining maximum forward speed with minimum sink speed. With a high body mass and associated high wing loading, they can reach relatively fast flight speeds, enabling access to prey resources that can be far from breeding colonies (Warham, 1977, Suryan et al., 2008).

Behaviourally, albatrosses exploit wind shear generated by gradients in surface and low altitude winds and pockets of lighter winds between waves, to achieve dynamic soaring flight, gaining momentum with little energetic expenditure (Sachs, 2005).

In terms of their life history strategy, albatrosses are extreme *K*-strategists; with long life expectancy, a slow breeding cycle and low fecundity (Warham, 1990). The combination of a long reproductive cycle and morphological traits that favour economic long-distant flight allows albatrosses to forage across vast areas to find patchily distributed prey (Lack, 1968). Furthermore, within the Southern Ocean, albatrosses are known to feed at oceanographic features that are far from their colonies, including mesoscale eddies (Nel et al., 2001) and frontal zones (Scales et al., 2015).

Variations in life history (e.g. longevity, breeding frequency, breeding- season duration) and morphology (e.g. body mass, wingspan, wing area) affect reproductive costs and aerodynamic performance of albatrosses, and, ultimately, their capacity to buffer the effects of environmental variability (Weimerskirch et al., 1986). Differences in flight costs may mean that species which expend more energy to reach distant foraging areas are more vulnerable to environmental stochasticity or, alternatively, species that exhibit greater behavioural flexibility in foraging are more resilient to ecosystem perturbations (Kappes et al., 2010).

Four species of albatross breed at subantarctic Macquarie Island (54.6° S, 158.9° E), black-browed *Thalassarche melanophris*, grey-headed *T. chrysostoma*, light-mantled *Phoebetria palpebrata* and wandering *Diomedea exulans*, representing three of the four genera of the albatross family. The populations within this community have differing long-term trends; two species are increasing (black-browed and light-mantled albatrosses), one decreasing (wandering albatrosses) and one with a stable population trajectory (grey-headed albatrosses) (DPIPWE, 2014). With different energetic costs associated with flight and reproduction (Chapter 1, Fig. 2), the four species are likely to have different core foraging areas. I aimed to: 1) determine the environmental features influencing habitat use and 2) understand how morphology and life history constraints influence foraging distribution and consequently, vulnerability or resilience to environmental variability.

Methods

Field data collection

Four species of albatrosses (black-browed, n = 10; grey-headed, n = 10; light-mantled, n = 15; and wandering albatrosses, n = 12) from Macquarie Island (54.6° S, 158.9° E) were tracked over their breeding and nonbreeding periods between November 1992 and December 2009 (Fig. 1 & Table S1) using global location sensing (GLS) tags (British Antarctic Survey, Cambridge, UK) or Platform Terminal Transmitters (PTTs; Microwave Telemetry, Columbia, USA). The GLS tags (4.5 g, 25x18x7 mm) sampled light each minute and stored the highest value at the end of each ten-minute period, and also recorded the water temperature after twenty minutes of saltwater immersion. The GLS tags were ground-truthed at the deployment location for six days before being deployed. These tags were attached to 40 mm plastic darvic bands using epoxy glue and a cable tie, then fastened to the tarsus of each individual while restrained off the nest. The PTTs (30 g, 50x15x15 mm) were attached to three small groups of feathers with Tesa© tape to the mantle region between the wings, with the antennae extending to the anterior of the bird (Wilson et al., 1997, Terauds et al., 2006a). The PTTs were programmed to transmit every 90 seconds.

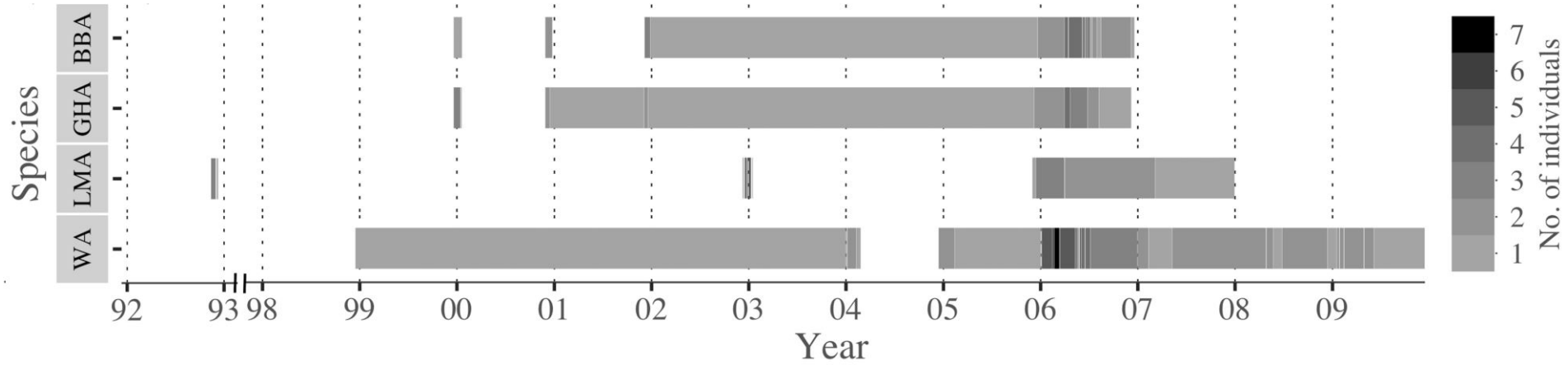

Figure 1 Timeline of Platform Terminal Transmitters (PTT) and Global Location Sensing (GLS) tag deployments on black-browed (BBA, n = 10), grey-headed (GHA, n = 10), light-mantled (LMA, n = 15) and wandering albatrosses (WA, n = 12) from Macquarie Island showing temporal changes in the number of individuals tracked.

Data processing

The GLS tag data were extracted and decompressed using BASTrak software (*Communicate and Decompressor*). Subsequently, twice-daily locations were estimated using the R packages, *SGAT* and *BAStag* (https://github.com/SWotherspoon/SGAT, https://github.com/SWotherspoon/BAStag). Geolocation is more accurate if it is based on unobstructed sampling of light data during the twilight periods, which allows the determination of sunrise and sunset times. However, it is common for light records from birds to exhibit shading by feathers or nesting behaviour, which may delay or advance the estimated timing of sunrise or sunset, respectively. A pre-processing step was implemented to minimise the effects of shading. By identifying the onset or end of twilight as the crossing of a set threshold light level, I could interactively assess whether the light data were free of shading. Occasions where shading of the light disrupted the onset of the recorded twilight were advanced or retracted to the correct twilight time only if the shading ceased before the end of the twilight.

Initial twilight times were determined using the threshold method applied to pre-processed light data and locations estimated at local noon and midnight (Hill and Braun, 2001, Ekstrom, 2004). A Bayesian framework was used to estimate the most likely location (and 95% CI) using light data and a set of three priors. The first prior was used to constrain consecutive locations and consisted of a gamma distribution of observed speeds with a maximum straight-line travel speed between two twilight locations (sunrise/sunset) set as 90 km/hr. The second prior addressed unresolvable shading and composed of a beta distribution of twilight errors (in minutes from actual twilight). The final prior included remotely-sensed sea surface temperature with a Gaussian distribution. Erroneous high temperatures were excluded during pre-processing. Locations of tagged albatrosses that encountered 24-hour daylight during the polar summer were constrained to regions south of a maximum latitude based on predicted photoperiods. For GLS tag data that showed irreconcilable noise in the light data (n = 4), an alternative new method was used to estimate location (https://github.com/ABindoff/geolocationHMM). The "twilight-free" method matches an overall daily pattern of light and SST with expected light and remotely sensed SST at each cell on a regularly spaced global grid. A fundamental assumption is that the sensor can be shaded during daylight hours, but cannot record light during night hours. Therefore, for any cell where light is observed when dark would be expected can be ruled out. A likelihood of the observer being in the remaining cells is then calculated according to the length of time

that the sensor would need to be shaded for the light record to have been observed in each cell. A symmetric forwards-backwards algorithm then determines a time-series of the most likely positions (95% CI) with plausible restrictions on movement.

The PTT locations in Argos location class "Z" were removed, and the remainder filtered according to flight speed using a forward-backward averaging algorithm based on the maximum travel speed (McConnell et al., 1992), using the R package *trip* (Sumner et al., 2009). All data processing and analysis were completed within R: A language and environment for statistical computing (R Core Team, 2016).

Statistical analysis

Residence time was estimated by first calculating the time spent by each tracked bird in each 100 km square cell, then taking the average of these values for each cell across all individuals. This avoids "halo" effects around breeding sites resulting from high aggregate residence times in nearby cells due to the many transits, albeit brief, by commuting birds. Prior to inclusion in the residence time analysis, the processed PTT and GLS locations were combined, and a half-hourly interpolation applied to capture use of cells corresponding to each individual track. The relatively coarse scale of the square grid cells enables PTT and GLS datasets to be integrated and analysed in the same way. I used the presence of an egg or chick in the nest to define the breeding period for each individual, with the nonbreeding period commencing at fledging or nest failure. The timing of laying, failure or fledging was established through regular nest monitoring and examination of the light data from the GLS tags (with incubation and guard periods easily identifiable from the frequent periods of shading). Tracking data from PTTs deployed on two juvenile black-browed, grey-headed and wandering albatrosses were combined with the data from nonbreeding adults in the residence time analysis, as their movements would have been similarly unconstrained by the demands of breeding. Despite differences in foraging behaviour and experience between juveniles and adults, juvenile albatrosses are likely to be similarly constrained by morphology influencing flight and foraging efficiency to adults during the nonbreeding period (Wunderle, 1991, Fayet et al., 2015). Furthermore, juvenile albatrosses previously tracked following fledging (as in this study) displayed habitat overlap with adults and similar flight paths and behavioural characteristics (De Grissac et al., 2016). For comparison, tracking data from juvenile albatrosses included in the nonbreeding dataset from this study are presented in the Supporting Information, Fig. S1. Although black-browed, grey-headed and wandering

albatrosses show some sexual segregation at other sites (Shaffer et al., 2001, Phillips et al., 2004, Froy et al., 2015), due to the small number of deployments in our study, tracks from male and female albatrosses were pooled in the analysis (Fig. S2). For nonbreeding black-browed, grey-headed and light-mantled albatrosses, the tracking data include in the analysis represents a small number of deployments (n = 4, n = 4, n = 2, respectively) and is unlikely to be representative of the distribution of the population.

To identify the environmental characteristics of the areas used by the albatrosses, I used generalised additive models (GAMs) with a log link, gamma distribution and maximum likelihood (ML) smoothness selection to the time spent grids. Daily oceanographic and atmospheric data (chlorophyll a concentration, eddy kinetic energy, bathymetric gradient, sea surface temperature gradient, sea surface height anomaly and wind speed) extracted from global databases and averaged over the parent grid cells from the spatial and temporal domain of interpolated tracking data for each species and period were included as the explanatory variables (Table S2). Oceanographic features such as frontal zones and eddy features were represented in the models as regions of higher sea surface temperature gradient, eddy kinetic energy and sea surface height anomaly. As the data were highly skewed, the covariate eddy kinetic energy was log-transformed. A latitude, longitude smoothed term was included as a covariate to account for spatial structure and spatial autocorrelation in the data. This method represents one of several approaches to dealing with autocorrelation in tracking datasets, which if left unaddressed can lead to errors in interpreting ecological relationships (Dormann, 2007, Hawkins, 2012). The trade-off for implementing this method is that some environmental relationships may remain unidentified because the spatial smoother explains a large amount of variability (Webb et al., 2014).

The correlations between predictor terms were investigated using a Pearson's correlation matrix, and a threshold of 0.8 was applied to remove highly correlated terms. Separate models were built for each species and period (breeding *vs.* nonbreeding season), incorporating all environmental predictors, followed by a stepwise model selection process, where the least significant terms were sequentially dropped, and the model refitted.

Results

Breeding period

During the breeding period, all species displayed constrained central-place foraging with a predominant north-south distribution, with the capacity to disperse limited by the demands of incubation or chick-rearing at the colony (Fig. 2a). Mean daily travel distances calculated from the filtered tracking data varied among species, with the smallest distances covered by wandering albatrosses (mean: 191± 8 km day^{-1}) and the largest by grey-headed and light-mantled albatrosses (respective means: 427± 18 km day^{-1}, 404± 12 km day^{-1}; Tukey's: $p = 0.66$; ANOVA: $F_{3, 2664} = 99.71$, $p < 0.001$). Contrasting patterns in the daily maximum distance from the colony showed black-browed albatrosses had higher residence times closer to Macquarie Island (mean: 326 ± 22 km), compared to wandering albatrosses, which typically foraged further from the island (mean: 942 ± 21 km) (ANOVA: $F_{3, 2664} = 110.1$, $p < 0.001$). The greatest overlap in distribution among species was along the Macquarie Ridge and into the Tasman Sea (Fig. 3a, Fig. S3)

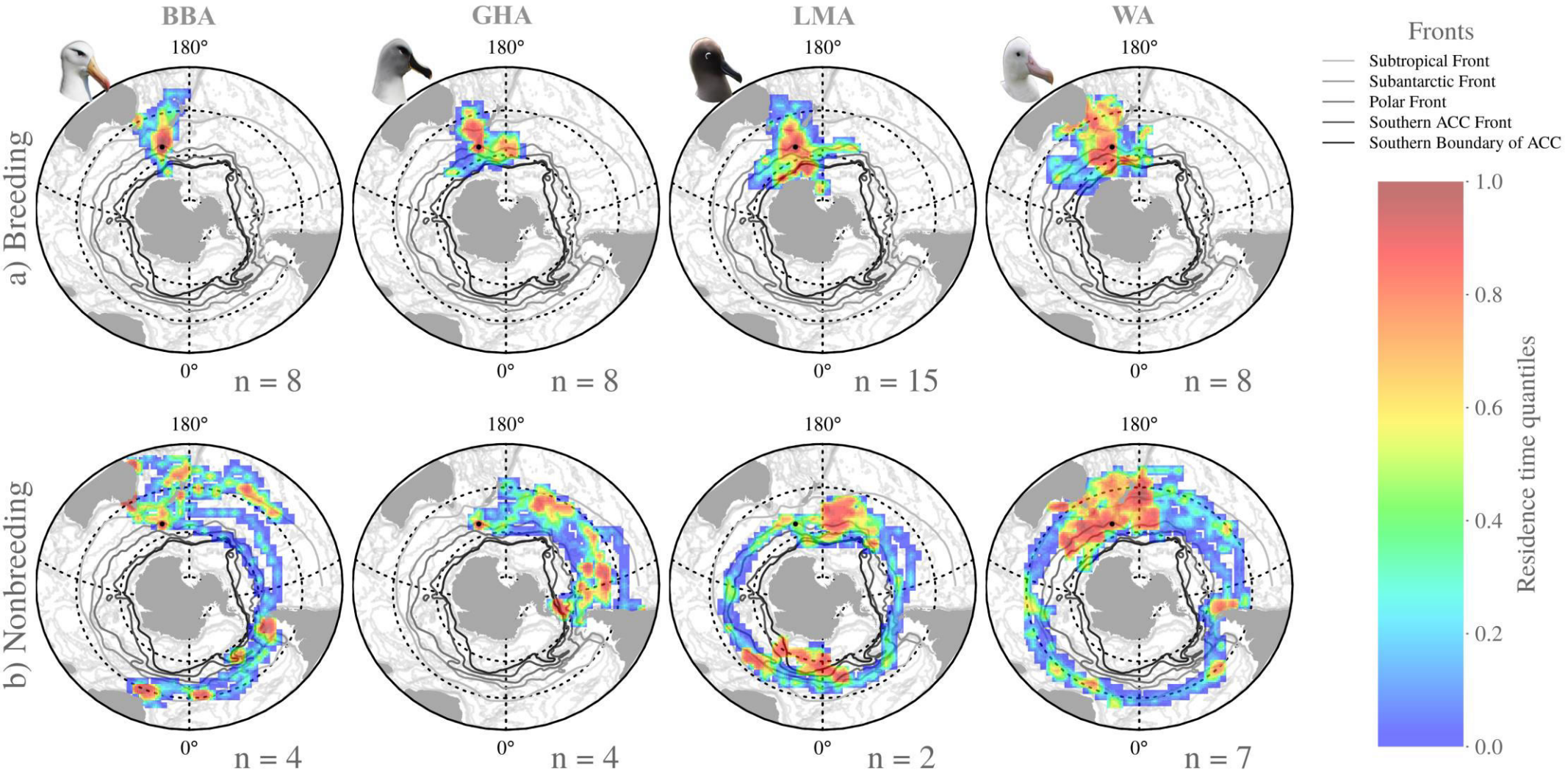

Figure 2 Residence time quantiles of black-browed (BBA), grey-headed (GHA), light-mantled (LMA) and wandering albatrosses (WA) tracked from Macquarie Island during the a) breeding and b) nonbreeding periods. Residence time was based on a 100 x 100 km grid. The major Southern Ocean frontal features are based on Orsi *et al.* (1995).

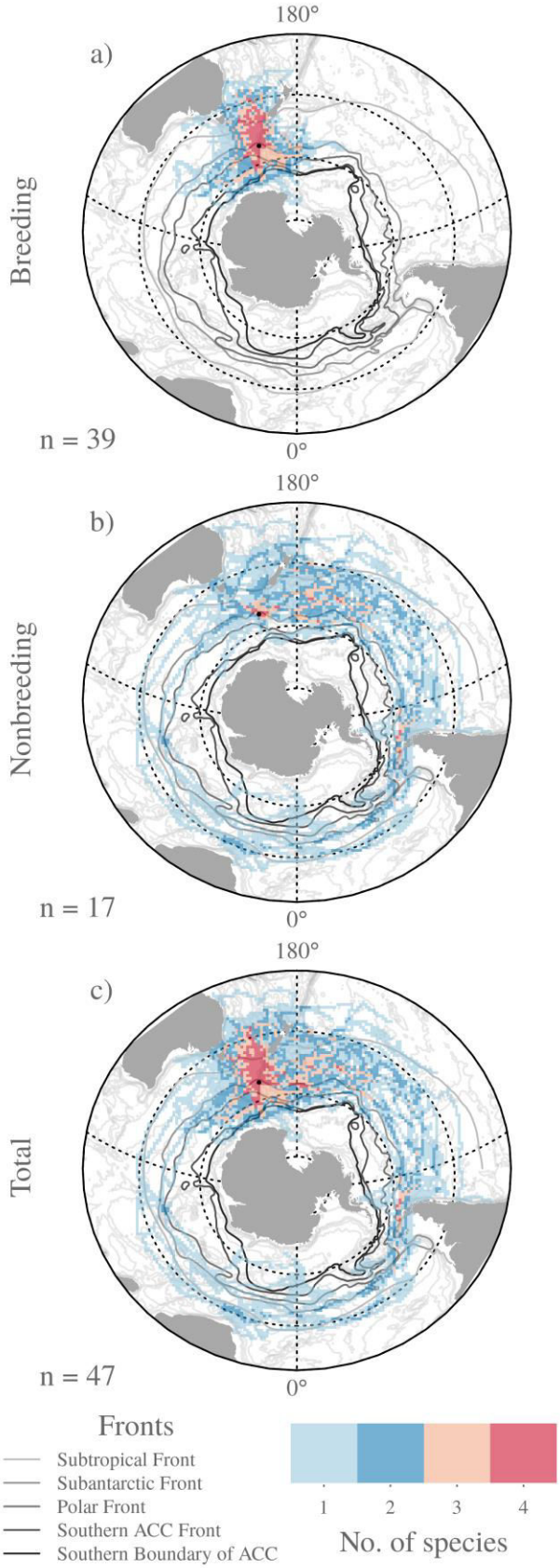

Figure 3 a) Breeding, b) nonbreeding and c) total species overlap of albatrosses tracked from Macquarie Island (black-browed, grey-headed, light-mantled and wandering albatrosses) (on a 100 x 100 km grid) in relation to major Southern Ocean frontal features (from Orsi *et al*. 1995).

For breeding black-browed albatrosses, the best model showed that high sea surface temperature gradient, high sea surface height anomaly, and moderate wind speeds best explained higher residence times during breeding (Fig. 4 & Table 1) where foraging occurred proximate to the breeding colony, primarily around the Subantarctic Front (SAF) (Fig. 5) at Macquarie Ridge and extending north into the south Tasman Sea (Fig. 2a, Fig. S3). Black-browed albatrosses covered a mean distance of 266 ± 13 km day^{-1} (Table 2). Of the four albatross species on Macquarie Island, this species has the lowest glide ratios, the shortest incubation shifts and chick-rearing period, and the lowest mean breeding success (Table 2).

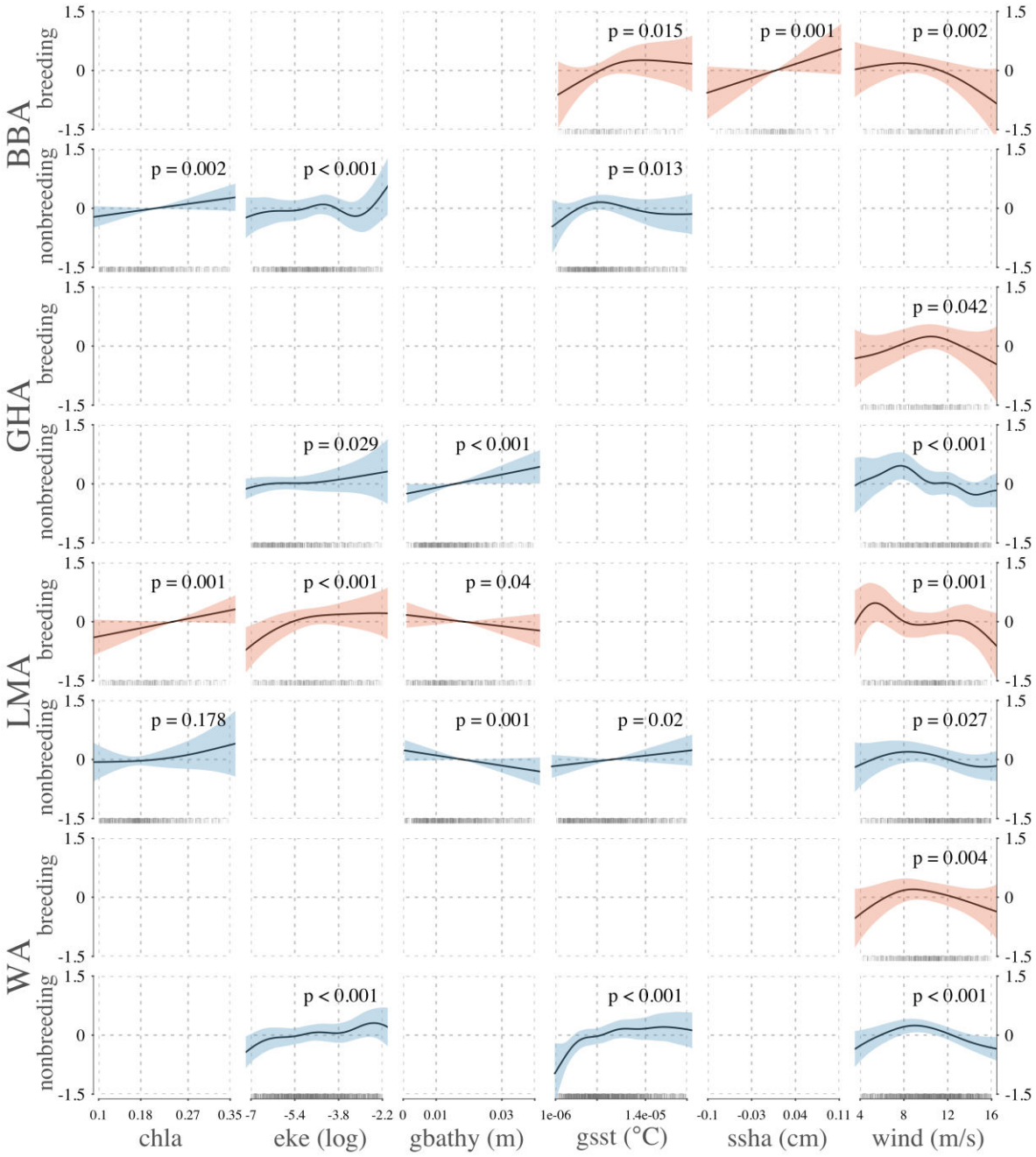

Figure 4 General additive model response curves (with shaded standard errors) showing significant relationships between residence time (hours) of breeding (red) and nonbreeding (blue) black-browed (BBA), grey-headed (GHA), light-mantled (LMA) and wandering albatrosses (WA) tracked from Macquarie Island, and environmental variables; chlorophyll a concentrations (chla), eddy kinetic energy (eke), bathymetric gradient (gbathy), sea surface temperature gradient (gsst), sea surface height anomaly (ssha) and wind speed (wind).

Table 1 General additive model results showing significant relationships between residence time (hours) of black-browed (BBA), grey-headed (GHA), light-mantled (LMA) and wandering albatrosses (WA) tracked from Macquarie Island, and environmental variables; chlorophyll a concentrations (chla), eddy kinetic energy (eke), bathymetric gradient (gbathy), sea surface temperature gradient (gsst), sea surface height anomaly (ssha) and wind speed (wind).

	Species	Smoothed term	Estimate	F	t	p	R^2	Deviance
BREEDING	BBA	intercept	10.1875		186.1937		0.2706	0.8512
		long. lat.		15.5791		<0.001		
		ssha		11.0138		0.0011		
		wind		4.8871		0.0023		
		gsst		3.5673		0.015		
	GHA	intercept	10.3509		175.9226		0.0233	0.6299
		long. lat.		8.7488		<0.001		
		wind		2.4716		0.0418		
	LMA	intercept	10.6691		253.1974		0.4268	0.6302
		long. lat.		19.0563		<0.001		
		eke (log)		6.8701		<0.001		
		chl		11.9919		<0.001		
		wind		3.3481		0.0015		
		gbathy		4.2591		0.0397		
	WA	intercept	10.9249		213.037		0.0647	0.5268
		long. lat.		14.9203		<0.001		
		wind		3.7916		0.004		
NONBREEDING	BBA	Intercept	10.0548		278.537		0.2276	0.4873
		long. lat.		13.3514		<0.001		
		eke (log)		4.8312		<0.001		
		chl		9.8216		0.0017		
		gsst		3.0436		0.0132		
	GHA	intercept	10.4761		295.4269		0.219	0.4102
		long. lat.		13.0776		<0.001		
		wind		5.4755		<0.001		
		gbathy		15.8203		<0.001		
		eke (log)		2.6937		0.0287		
	LMA	intercept	10.2028		252.5517		0.2235	0.5247
		long. lat.		23.0428		<0.001		
		gbathy		11.3853		<0.001		
		gsst		5.4396		0.0199		
		wind		2.4211		0.0273		
		chl		1.6085		0.178		
	WA	intercept	10.8688		376.1416		0.233	0.5037
		long. lat.		43.114		<0.001		
		wind		9.6689		<0.001		
		gsst		5.8276		<0.001		
		eke (log)		5.3217		<0.001		

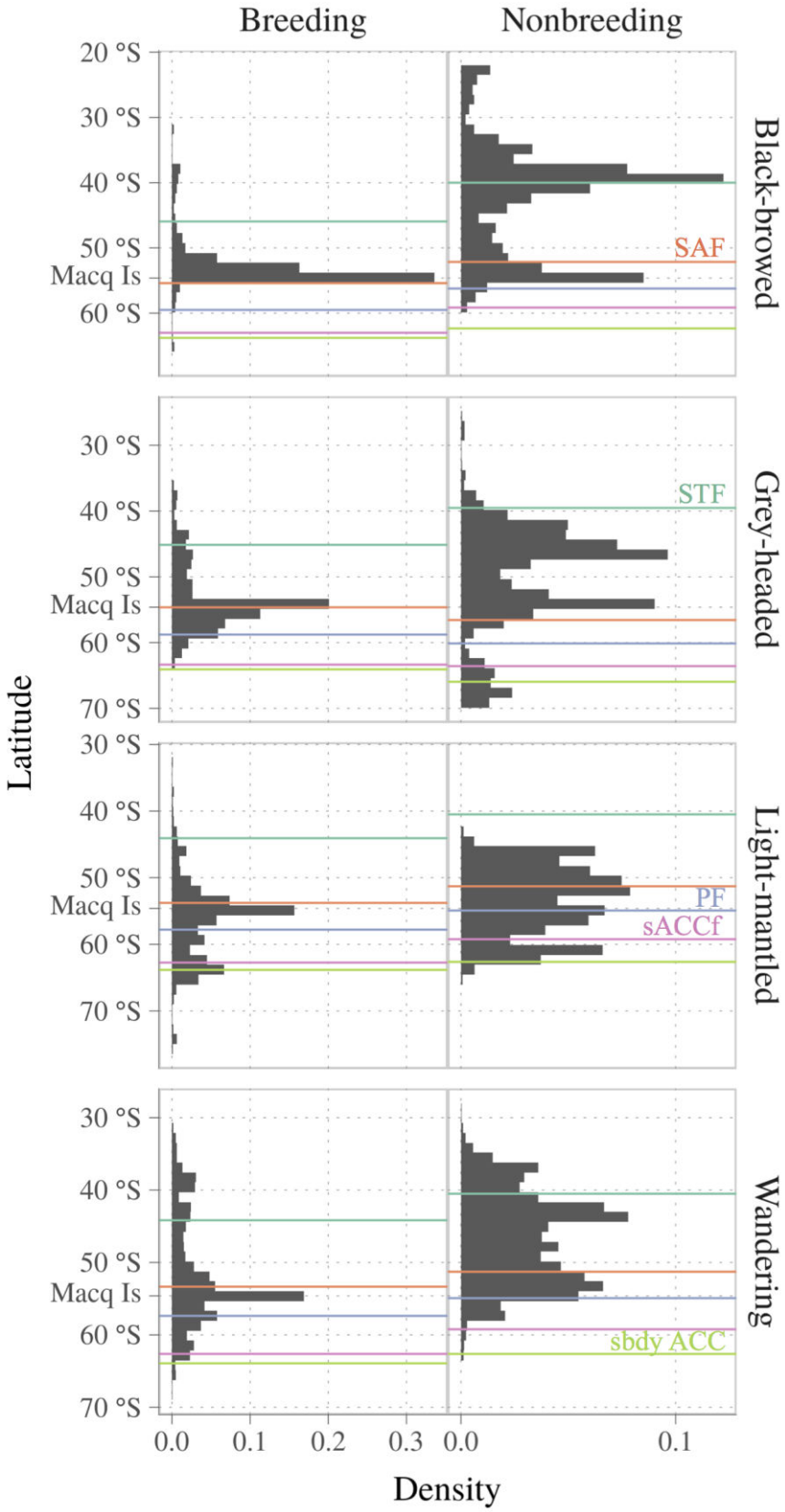

Figure 5 Histogram of locations of tracked breeding and nonbreeding albatrosses from Macquarie Island by latitude, in relation to the mean positions of major Southern Ocean frontal systems, averaged across the species distribution including the Subtropical Front, STF; Subantarctic Front, SAF; Antarctic Polar Front, PF; Southern Antarctic Circumpolar Current Front, sACCf; and the southern boundary of the Antarctic Circumpolar Current, sbdy ACC (from Orsi *et al*. 1995).

Table 2 Summary of functional and life history parameters of black-browed, grey-headed, light-mantled and wandering albatrosses. Values are means ± SE.

	Attribute	Black-browed	Grey-headed	Light-mantled	Wandering	Reference
Status	Breeding pairs (2013/14)	44	88	2151	7	(DPIPWE, 2014)
	Population trend	increasing	stable	increasing	decreasing	
Physiology	Mass (kg)**	M: 3.67±0.23 F: 3.05±0.17	M: 3.52±0.25 F: 3.07±0.18	2.84	M: 9.44±0.59 F: 7.84±0.18	(Pennycuick, 1982, Shaffer et al., 2001, Phillips et al., 2004)
	Wingspan (cm)**	M: 228.8±5.3 F: 221.8±3.4	M: 221.2±4.0 F: 216.0±5.5	218	M: 311.0±4.0 F: 299.0±5.0	
	Wing area (cm^2)	M: 3900±150 F: 3660±90	M: 3555±130 F: 3395±135	3380	M: 6260±270 F: 5860±230	
	Wing loading**	M: 92.3±5.3 F: 81.7±4.0	M: 97.1±7.0 F: 88.6±5.9	82.4	M: 148.0±10.0 F: 132.0±11.0	
	Aspect ratio**	M: 13.4±0.3 F: 13.4±0.3	M: 13.8±0.3 F: 13.8±0.5	14.1	M: 15.5±0.6 F: 15.3±0.6	
	Maximum glide ratio	21.7	22.0	22.4	23.2	
Reproduction	Breeding frequency	annual	biennial	biennial to triennial	biennial	(Terauds, 2002)
	Breeding season	late Sept – early May	early Oct – late May	mid Oct – mid June	early Dec – early Jan (13 months)	
	Laying date	25 Sept – 31 Oct	6 Oct – 30 Oct	Oct – 17 Nov	8 Dec – 14 Jan	
	Early incubation shift length (days)	3.1±0.1	5±0.2	NA	8.8±0.4	
	Late incubation shift length (days)	3.6±2.7	7.5±4.0	10.5±4.6	8.8±4.9	
	Mean incubation length (days)	68.9±0.2	71.7±0.1	66.5±0.3	79.2±0.2	
	Mean brood guard length (days)	22.4±0.4	24.8±0.3	22.4±0.5	30.1±0.8	
	Chick rearing length (days)	118*	135*	139.7±2.6	273.6±3.6	
	Mean breeding success (1994 – 2014)	43.4±12.4	52.0±12.5	48.6±12.3	63.85±19.8	(DPIPWE, 2014)
Foraging	Mean distance travelled (breeding, km day^{-1})	266.2±12.7	426.5±17.5	403.8±12.4	191.1±8.1	This study
	Mean distance travelled (nonbreeding, km day^{-1})	351±14	266±9	265±11	153±4	
	Daily (breeding period) maximum distance from the colony (km)	326±22	812±35	811±23	942±21	

*median values **data from colonies other than Macquarie Island

Grey-headed albatrosses also had high residence times in the Tasman Sea and the SAF to the east of Macquarie Island (Fig. 2a, Fig. S3), with the latter used by seven of eight tracked individuals, all of which displayed direct flight followed by high residence time in the region. The best species distribution model included only wind speed, with moderate speeds corresponding to higher residence times, and no significant effect of any of the oceanographic covariates (Fig. 4 & Table 1). Grey-headed albatrosses travelled considerably greater mean daily distances than black-browed albatrosses, but also have a higher aspect ratio and wing loading and subsequent glide ratios, longer incubation shifts, and a longer breeding season (Table 2).

Light-mantled albatrosses showed the broadest breeding distribution, the most southerly range, and concentrated their time over frontal regions including the Antarctic Polar Front (APF) to the south of Macquarie Island and the southern boundary of the Antarctic Circumpolar current (ACC) (Fig. 5, Fig. S3). For light-mantled albatrosses, high chlorophyll-a concentrations, high eddy kinetic energy, low bathymetric gradient and low to moderate wind speeds best-explained residence time (Fig. 4 & Table 1). This species travelled large distances each day during the breeding period (Table 2). Compared to the two *Thalassarche* species, light-mantled albatrosses have a high aspect ratio, low wing loading, superior glide ratios, the longest incubation shifts (although a shorter incubation period), and a longer chick-rearing period (Table 2).

Habitat use by wandering albatrosses during the breeding season was predominantly to the west of Macquarie Island (Fig. 2a). The best models for this species included only wind speed, and no oceanographic covariates had a significant effect on residence time during the breeding period (Fig. 4 & Table 1). Of the four species, wandering albatrosses travel furthest from the colony at the slowest speeds, have the longest incubation, brood-guard and chick-rearing periods, and the highest aspect ratio and wing loading (Table 2). Wandering albatrosses have consistently long incubation shift lengths during both the early and late incubation phases, which are only exceeded by light-mantled albatrosses in late incubation.

The single consistent covariate in the best habitat models for residence time across all species was wind speed, with moderate wind strength corresponding to high residence times (Fig. 4 & Table 1). Despite broad similarities in breeding distribution and response to wind speed, the best models for each species contained different environmental covariates.

Nonbreeding period

All species dispersed much more widely during the nonbreeding period and had patchy density-distributions characterised by isolated areas of high residence time (Fig. 2b). Despite the larger overall distribution, the daily distances were significantly shorter than those during the breeding period for all species, except black-browed albatrosses, which displayed a mean daily flight distance of 351 ± 14 km day^{-1} (32.0% greater than during the breeding period) [ANOVA: $F_{3, 7143} = 49.02$, $p < 0.001$]. Wandering albatrosses covered the shortest daily distances (mean: 153 ± 4 km day^{-1}) and black-browed albatrosses the greatest distances. As in the breeding period, grey-headed and light-mantled albatrosses covered comparable distances (respective means: 265 ± 9 km day^{-1}, 265 ± 11 km day^{-1}; Tukey's: $p = 0.66$; ANOVA: $F_{3, 4479} = 128.8$, $p < 0.001$). Overlap of all four species (corresponding use of individual 100 x 100km grid cells), was restricted to a small region close to the breeding colony and several isolated groups of grid cells in the south-west Pacific basin and the Drake Passage (Fig. 3b). The limited overlap during the nonbreeding period is likely attributable to the small number of individuals tracked and the expansive foraging ranges of each species.

During the nonbreeding period the best habitat models included multiple environmental covariates and showed that despite vast differences in spatial habitat use, higher residence times were associated with similar oceanographic features (Fig. 4 & Table 1). Furthermore, the relationship of residence time to wind speed was similar to the breeding period for grey-headed, light-mantled and wandering albatrosses, with a general pattern of moderate winds corresponding to higher residence time (Fig. 4 & Table 1). Despite some similarities, the species distribution models did detect differences among species in the response to environmental covariates. As annual breeders, with the shortest nonbreeding period of all four species, black-browed albatrosses had highest residence times in isolated regions of

high chlorophyll a concentration, eddy kinetic energy and sea surface temperature gradient (Fig. 4 & Table 1).

For tracked grey-headed albatrosses, high eddy kinetic energy and bathymetric gradient were the best predictors of high residence time (Fig. 4 & Table 1), reflecting the habitats used in the central southern and south-east Pacific basin, south of the Subtropical Front (STF) (Fig. 5, Fig. S3). One tracked individual showed extended residence time south of 63°S at the southern boundary of the ACC off the western Antarctic Peninsula. Grey-headed albatrosses showed similar mean daily flight distances and duration to light-mantled albatrosses during the nonbreeding period, although they utilised quite different foraging areas (Table 2). However, there was a discernible contrast in their response to bathymetric gradient, showing positive and negative linear relationships for grey-headed and light-mantled albatrosses, respectively (Fig. 4 & Table 1). Of the two tracked nonbreeding light-mantled albatrosses, one showed a circumpolar distribution, and the other may have completed a circumpolar movement; however, the geolocator failed at approximately 10°W. High residence times by the tracked light-mantled albatrosses were associated with high chlorophyll a concentrations, high eddy kinetic energy and low bathymetric gradient (Fig. 4 & Table 1) in the central southern Pacific and south-east Atlantic oceans (Fig. 2b).

Wandering albatrosses covered the shortest mean daily distances during the nonbreeding period (Table 2) with highest residence times in areas of higher eddy kinetic energy and sea surface temperature gradients (Fig. 4 & Table 1) in the south-west Pacific basin, close to the breeding colony (Fig. 2b). Six of the seven individuals tracked showed a broadly resident migration strategy with high use of the south-west Pacific basin region. The remaining individual completed two circumpolar navigations during one nonbreeding period; the first in 201 days and the second in 55 days.

Discussion

I built species distribution models for four sympatric albatross species during the breeding and nonbreeding periods to examine the relationships between habitat use and eco-morphological and life history traits. In so doing, I have improved our

understanding of the potential vulnerability of each species to environmental change. Foraging distances of the albatrosses tracked from Macquarie Island were limited during breeding by incubation and chick-rearing duties, which impose a central-place foraging constraint (Ashmole, 1963). This presumably explains the higher inter-specific overlap in habitat use at this time compared with the nonbreeding period. Foraging was predominantly around oceanographic features to the north of the colony, along transit corridors to the Macquarie Ridge, and north into the Tasman Sea. These features provide seasonally productive habitat (Tilburg et al., 2002, Sokolov and Rintoul, 2007), which are also used by other marine predators e.g., Macquarie Ridge; southern elephants seals *Mirounga leonina* (Hindell et al., 2016), and subantarctic *Arctocephalus tropicalis* and Antarctic fur seals *A. gazella* (Robinson et al., 2002), Tasman Sea; Buller's albatrosses *Thalassarche bulleri*, (Sagar and Weimerskirch, 1996, Stahl and Sagar, 2000a, Stahl and Sagar, 2000b), Cook's Petrel *Pterodroma cookii* (Rayner et al., 2008) and Antipodean (Gibson's) albatrosses *D. antipodensis gibsoni* (Walker and Elliott, 2006).

Despite high overlap during the breeding season, there were some inter-specific differences in habitat use. This may arise through the influence of morphological differences on flight costs, competitive exclusion, or variability in reproductive trade-offs. Differences in flight and activity patterns also appears to influence spatial segregation of these same species from South Georgia during the breeding and nonbreeding periods (Phillips et al., 2005a, Mackley et al., 2010). On Macquarie Island, species with adaptations for more energetically efficient flight (higher glide ratio, higher aspect ratio, less induced drag, increased lift), and with longer breeding periods, travelled further from the colony. Conversely, the species with higher flight costs (lower glide ratio, lower aspect ratio, greater induced drag, decreased lift) and a shorter breeding period foraged more locally. Their use of distinct oceanographic features therefore provides evidence of resource partitioning during the breeding period.

Black-browed albatrosses made use of local neritic waters associated with the Macquarie Ridgeline and the SAF. Neritic, shelf edge foraging is typical of this species at Macquarie Island (Terauds et al., 2006a) and other colonies (Cherel and Weimerskirch, 1995, Weimerskirch et al., 1997b, Wakefield et al., 2012). Despite

high residence time detected over the Macquarie Ridgeline, bathymetry was not detected as an important predictor in the analysis. Perhaps, this result is an artefact of scale, where shelf edge waters and associated steep gradient in bathymetry occur over a smaller scale than the 100km grid cell used in the modelling. The comparatively low aspect ratio of black-browed albatrosses results in higher drag during flight, more use of flap-gliding and increased energetic costs for long-distance travel (Pennycuick, 1982). Combined with a lower wing loading, which facilitates improved manoeuvrability and aerodynamic lift at lower wind speeds, black-browed albatrosses have greater take-off performance and are known to outcompete other albatross species for prey in multi-species feeding aggregations (Pennycuick, 1983, Harrison et al., 1991, Warham, 1977, Weimerskirch and Guionnet, 2002). This is reflected in their at-sea activity patterns; shorter flight bouts and a larger proportion of time spent on the water compared to the other species (Mackley et al., 2010). Localised foraging by black-browed albatrosses is coupled with faster recovery of adult body condition, shorter incubation shifts, and a higher meal delivery rate such that the chick-rearing period is shorter than in the other species (Huin et al., 2000, Waugh et al., 2000, Phillips et al., 2003).

In contrast, grey-headed albatrosses travel greater distances, have longer intervals between incubation shifts (Terauds, 2002) and chick feeds, and exhibit slower chick development (Huin et al., 2000, Waugh et al., 2000, Phillips et al., 2003). As at Macquarie Island, breeding grey-headed albatrosses at other sites also associated with large-scale frontal systems that represent regions of concentrated productivity and higher prey availability (Waugh et al., 1999a, Scales et al., 2015). Despite concentrated foraging along the SAF to the east of Macquarie Island, no relationship between residence time and sea surface temperature gradient was evident in the birds tracked from Macquarie Island, potentially due to the individual variability in foraging areas.

High residence times were associated with lower wind speeds in breeding light-mantled albatrosses than in the other species. Their considerably lower wing loading provides greater aerodynamic lift and more economic flight at lower wind speeds, allowing efficient foraging south of 61°S where wind speeds are lower and less consistent (Young, 1999). This is emphasised by their limited use of waters around

the APF (between 56°S and 61°S), where wind velocities are higher. Similarly, breeding birds tracked from Heard Island and South Georgia typically forage far south of the APF (Phillips et al., 2005a, Lawton et al., 2008). By undertaking long incubation shifts and employing a bimodal foraging strategy in chick-rearing (Terauds and Gales, 2006), light-mantled albatrosses from Macquarie Island can not only exploit local foraging habitat close to the colony but also make use of tailwinds to travel to distant, highly productive waters associated with the southern boundary of the ACC (Weimerskirch and Robertson 1994). In these waters, greater surface productivity promotes high densities of prey, including large, ephemeral aggregations of krill during the austral summer (Tynan, 1998).

Wandering albatrosses are much larger than the other species at Macquarie Island; consequently, the adults have greater energy reserves, and the chick has a longer fasting capability, enabling longer foraging trips by parents (Arnould et al., 1996, Berrow and Croxall, 2001). The slower travel speeds of the tracked birds and characteristic long looping flights reflect a foraging strategy that involves searching large areas to maximise encounters with patchily distributed prey (Weimerskirch et al., 1997c, Wakefield et al., 2009). Their high aspect ratio, wing loading and glide ratios support efficient dynamic soaring, enabling exploitation of distant resources at little energetic cost (Shaffer et al., 2001). However, these traits reduce efficiency during take-off and landing (Weimerskirch et al., 1997c, Mackley et al., 2010). Consequently, wandering albatrosses land less frequently than other albatrosses and remain on the water for longer periods (Croxall and Prince, 1994, Weimerskirch et al., 1997c, Mackley et al., 2010). The wandering albatrosses tracked from Macquarie Island took advantage of the prevailing westerly wind circulation of the Southern Ocean, which provides crosswinds for efficient flight (Wakefield et al., 2009).

During the nonbreeding period, when central-place constraints disappear, the use of broadly similar environmental features by all species tracked from Macquarie Island reflects both the patchy distribution of prey and their capacity to exploit a variety of oceanographic features where prey aggregate. Competition is reduced, and in the absence of central-place constraints, the influence of morphology on habitat use is likely to be more pronounced, associated with the greater spatial heterogeneity in

environmental conditions across large areas. Wind parameters may therefore drive niche segregation by affecting flight efficiency (Spear and Ainley, 1997b).

With no requirement to return to the colony, nonbreeding albatrosses from Macquarie Island concentrated at distant regions of elevated primary productivity (high chlorophyll a concentrations), mesoscale eddy structures (high eddy kinetic energy) and thermal fronts (high sea surface temperature gradient). Oceanic fronts were preferred by black-browed, light-mantled and wandering albatrosses, and mesoscale eddy structures by black-browed, grey-headed and wandering albatrosses. Both frontal regions and eddy structures can aggregate prey through physical structuring and concentration of primary productivity and zooplankton biomass, offering predictable resources for higher trophic-level predators (Mitchell et al., 1991, Sokolov and Rintoul, 2007, Bost et al., 2009).

Despite the small number of nonbreeding individuals tracked in our study, all four species overlapped in the south-east New Zealand Exclusive Economic Zone (EEZ), where light-mantled and wandering albatrosses, in particular, had high residence times. Here, the SAF tracks the subantarctic slope on the edge of the Campbell Plateau (Morris et al., 2001) meeting the STF; this creates a frontal region of high current velocity that continues eastwards and results in high surface eddy kinetic energy (Sallée et al., 2011) and high biological productivity (Murphy et al., 2001). By making use of prevailing westerly winds, Macquarie Island albatrosses can access this profitable region with low travel costs. This area is also used by Antipodean wandering albatrosses *D. antipodensis antipodensis* (Walker and Elliott, 2006), Campbell albatrosses *T. impavida* (Waugh et al., 1999a), Chatham petrels *P. axillaris* (Rayner et al., 2012) and southern elephant seals (Pascoe et al., 2016).

The annual-breeding black-browed albatrosses have a shorter nonbreeding period, travelled further overall, and flew further each day than the biennial-breeding species (grey-headed, light-mantled and wandering albatrosses). With a smaller temporal window in which to recover body condition, black-browed albatrosses are under greater pressure to move rapidly to productive habitat. The shorter nonbreeding period may explain their relatively low breeding success, reflecting carry-over effects from the previous breeding season (Crossin et al., 2016). With the lowest aspect ratio

and the highest glide ratio of the four species (Pennycuick, 1982), black-browed albatrosses utilise powered (flapping) flight more frequently and have shorter flight bouts (Mackley et al., 2010). Consequently, they are less reliant on consistent winds, allowing them to exploit waters associated with the STF, where winds are lighter than at higher latitudes in the Southern Ocean (Young, 1999). One individual spent a long period on the Patagonian Shelf and in the Benguela Upwelling off South Africa, which are both highly productive regions and represent core foraging areas of black-browed albatrosses from the Falkland Islands (Patagonian Shelf only; Wakefield *et al.* 2011) and South Georgia (Phillips et al., 2005b, Mackley et al., 2010). This excursion to the Benguela Upwelling represents an unusually long nonbreeding dispersal for this species, which tend to remain within local ocean basins.

Nonbreeding grey-headed albatrosses used waters between the SAF and the STF, with particularly high residence times in the south-east Pacific basin. There was considerable overlap west of Chile with conspecifics from Marion Island, but little with those from South Georgia (Clay et al., 2016). Like birds from Marion Island, but not South Georgia or Campbell Island (Waugh et al., 1999a, Clay et al., 2016), grey-headed albatrosses from Macquarie Island associated with steep bathymetric features such as shelf slopes, which potentially drive nutrient-rich upwelling and support high prey densities.

Nonbreeding light-mantled albatrosses favoured southerly waters between 15°W and 45°E, demonstrating their capacity to capitalise on high latitude summer productivity associated with the southern boundary of the ACC. They made circumpolar navigations, and like wandering albatrosses (this study, Weimerskirch *et al.* 2015) and grey-headed albatrosses (Clay et al., 2016) exploited the consistent westerly winds to travel long distances east at low cost.

Although they also have the capacity to disperse around Antarctica, nonbreeding wandering albatrosses from Macquarie Island had highest residence times in the south-west Pacific. Similarly, a proportion of birds from Crozet and Kerguelen remain resident within the breeding range during the nonbreeding season (Weimerskirch et al., 2015). The nonbreeders from Macquarie used the nearby SAF, or showed a sedentary-with-excursions strategy, making occasional movements to the Campbell

Plateau, which also represents a core foraging area for nonbreeding wandering albatrosses from Kerguelen (Weimerskirch et al., 2015). Other birds from Macquarie Island migrated to the Humboldt Upwelling, an area well known for its high biological productivity and diversity of seabirds, including several migrant albatross and petrel species from New Zealand (Spear et al., 2003, Nicholls et al., 2005, Walker and Elliott, 2006, Landers et al., 2011), and a proportion of white-chinned petrels from South Georgia (Phillips et al., 2006). Furthermore, there was less evidence of relationships between residence time and environmental variables for nonbreeding wandering albatrosses compared to the smaller albatross species; this suggests broader habitat preferences, perhaps associated with their large energy reserves and efficient flight morphology.

This study presents the entirety of albatross tracking data from Macquarie Island collected to date, comprising a small number of deployments over several years. Although there was some overlap among species in habitat use across both the breeding and nonbreeding periods, there was also evidence for spatial segregation and foraging niche specialisation (i.e., preferences for particular oceanographic features). This is in agreement with a previous study (Mackley et al., 2010) of at-sea activity patterns of the same four species tracked from South Georgia during the nonbreeding season. Although our small samples make it difficult to make population-level inferences about core distributions, the differences in habitat preferences corresponded well with the differences among species in life history, and their morphological adaptations.

Resilience to climate change

For Southern Ocean albatrosses, the consequences of unprecedented global warming and consequent changes in oceanographic and atmospheric conditions are uncertain. However, differences in morphology and life history among species, and hence their behavioural flexibility, are likely to determine their resilience (Jiguet et al., 2007, Maloney et al., 2009, Ficetola et al., 2016). The consistent use of waters to the north of Macquarie Island by breeding black-browed albatrosses may increase vulnerability to climate-induced changes in the latitude of the SAF. The easterly meander of the SAF interacts with the Macquarie Ridge, a region of steep bathymetric gradient running northeast-southwest and generating strong upwelling, which elevates summer

chlorophyll concentrations (Sokolov and Rintoul, 2007), generates eddies (Rintoul et al., 2014) and may support higher trophic connections through entrainment of phytoplankton (Shuckburgh et al., 2009, d'Ovidio et al., 2013). As identified by Flynn and Williams (2012), a southerly shift in the position of the SAF (Sokolov and Rintoul, 2009) could result in high flow velocities to the south of the Macquarie Ridge Gap, reducing down-flow mixing and, potentially, surface productivity in the region.

For three species (not nonbreeding black-browed albatrosses), higher residence times were linked to moderate wind speed. This reflects the balance between enough wind to facilitate aerodynamic lift, and the avoidance of extreme wind speeds that hinder manoeuvrability, in order achieve economic flight (Jouventin and Weimerskirch, 1990). Alternatively, high wind speeds may reduce the capacity of albatrosses to locate food by reducing the ability to detect olfactory cues and the visibility of surface prey. The dependence of albatrosses from Macquarie Island on moderate wind regimes may make them vulnerable to climate-induced changes in wind patterns as the Southern Annular Mode (SAM) becomes increasingly positive (Marshall, 2003). In the positive SAM phase, the band of Antarctic circumpolar winds contract towards the Antarctic continent resulting in relaxed mid-latitudinal winds (Hall and Visbeck, 2002). Intensified Antarctic circumpolar winds associated with a continuing positive trend in the SAM have benefited wandering albatrosses from Crozet Isles by reducing the energetic cost of reaching distant foraging areas, resulting in higher breeding success and body mass (Weimerskirch et al., 2012). For light-mantled albatrosses and breeding wandering albatrosses from Macquarie Island, which target high-latitude waters, a southward shift in wind intensity may prove beneficial by lowering flight costs. However, for breeding black-browed albatrosses, which rely on the Macquarie Ridge and Tasman Sea, and nonbreeding grey-headed and wandering albatrosses that predominantly use waters north of the SAF, a reduction in meridional wind and wind speeds at lower latitudes could reduce flight efficiency and increase energetic costs, presumably with repercussions for breeding performance.

Conclusions

The habitat use of albatrosses from Macquarie Island reflects foraging strategies that are shaped by functional morphology and life history adaptations. The two extremes

are a wide-ranging search strategy (wandering albatrosses), which maximises encounter rate with dispersed prey, and a rapid-transit strategy (black-browed, grey-headed and light-mantled albatrosses), whereby individuals forage at oceanographic features associated with more predictable prey. The resulting differences in core foraging areas have important implications for susceptibility to environmental change. For example, black-browed albatrosses, with a more northerly distribution, lower flight efficiency and greater reliance on local productivity, are predicted to be at greater risk of climate-driven shifts in wind patterns and frontal systems. Understanding the links between foraging behaviour, morphology and life history, and the vulnerability or resilience of Southern Ocean albatross species to current and predicted climate-driven atmospheric and oceanographic changes, has the potential to substantially improve forecasts of population viability for a range of seabird species.

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The authors would like to thank Rosemary Gales for her commitment to albatross monitoring on Macquarie Island over the last two decades, Graham Robertson for the contribution of historical light-mantled albatross tracking data, and field personnel involved in the logger deployments. All fieldwork was conducted under Standard Operating Procedures approved by the Tasmanian Department of Primary Industries, Parks, Water and Environment Animal Ethics Committee (Permit no. TFA16195, TFA15205, TFA14205, TFA13964, TFA12198).

Supporting Information

Table S1 Summary of GLS and PTT deployments on albatrosses from Macquarie Island between 1992 and 2009. Mean daily fixes are reported with standard error.

Species	Sex	Status	Band number	Device type	Device ID	Deployment date	Days tracked	Total fixes	Mean daily fixes
Black-browed albatross	F	adult	12143525	GLS	1203	30/11/05	384	352	1.01 ± 0.00
	M	adult	12139115	GLS	1187	21/12/05	350	703	2.00 ± 0.01
	F	adult	12139117	PTT	20876	20/12/99	31	458	14.31 ± 0.54
	M	adult	12139116	PTT	20877	28/11/00	28	291	10.39 ± 0.52
	F	adult	12112802	PTT	20875	28/11/00	29	256	8.53 ± 0.46
	M	adult	12139337	PTT	14418	2/12/01	25	684	26.31 ± 1.62
	F	adult	12139019	PTT	20877	2/12/01	27	678	24.21 ± 1.33
	M	adult	12119005	PTT	14257	6/12/01	21	445	20.23 ± 1.13
		juvenile	12149404	PTT	37467	1/4/06	96	735	7.66 ± 0.25
		juvenile	12149617	PTT	20877	1/4/06	96	760	7.92 ± 0.46
Grey-headed albatross		adult	12139225	GLS	1191	30/11/05	251	253	1.00 ± 0.00
		adult	12138972	GLS	1192	8/12/05	364	733	2.01 ± 0.01
	F	adult	12112695	PTT	20875	20/12/99	25	322	12.38 ± 0.46
	F	adult	12118905	PTT	20874	20/12/99	26	203	7.52 ± 0.65
	M	adult	A0409*	PTT	20877	20/12/99	30	455	14.68 ± 0.63
		adult	12139051	PTT	20876	28/11/00	17	219	12.17 ± 0.53
	F	adult	A0404	PTT	20874	28/11/00	27	225	8.04 ± 0.47
	M	adult	A0409*	PTT	14403	2/12/01	16	479	28.18 ± 0.8
		adult	unbanded	PTT	20875	4/12/01	18	440	23.16 ± 1.71
		juvenile	12149681	PTT	14257	1/4/06	21	146	6.64 ± 0.62
		juvenile	12149682	PTT	14418	1/4/06	86	660	7.59 ± 0.32
Light-mantled albatross		adult	12063972	GLS	1198	1/12/05	759	763	1.00 ± 0.00
		adult	12146141	GLS	1195	14/12/05	108	217	1.99 ± 0.01
		adult	12025901	GLS	1186	14/12/05	448	899	2.00 ± 0.00
		adult	unbanded	PTT	12606	13/11/92	17	182	10.11 ± 1.05
		adult	unbanded	PTT	12609	13/11/92	21	170	7.73 ± 0.85
		adult	unbanded	PTT	12604	13/11/92	25	281	10.81 ± 0.63
		adult	unbanded	PTT	12606	2/12/92	8	68	7.56 ± 1.88
		adult	12143641	PTT	37468	9/12/02	4	108	21.6 ± 2.94
		adult	12139296	PTT	37467	9/12/02	15	712	44.5 ± 2.92
		adult	12138851	PTT	14257	12/12/02	16	731	43.00 ± 3.61
		adult	12139525	PTT	14418	15/12/02	29	1076	38.43 ± 3.33
		adult	A1084	PTT	20877	15/12/02	32	1255	38.03 ± 2.72
		adult	12110945	PTT	37468	16/12/02	24	742	29.68 ± 3.09
		adult	12145258	PTT	37467	24/12/02	23	791	32.96 ± 3.72

		adult	12143650	PTT	14257	31/12/02	11	341	28.42 ± 3.67
Wandering albatross	M	adult	14030938	GLS	2123	16/12/98	51	54	1.04 ± 0.03
	F	adult	14052756	GLS	1200	30/11/05	1474	1490	1.01 ± 0.00
	F	adult	14030500	GLS	1190	3/1/06	1249	1093	1.01 ± 0.00
	M	adult	14049634	GLS	1194	4/1/06	360	727	2.01 ± 0.01
	F	adult	14030935	PTT	43921	29/12/03	41	1079	26.32 ± 0.88
	F	adult	14030908	PTT	43922	1/1/04	55	1697	30.3 ± 0.73
	M	adult	14052748	PTT	37388	3/1/06	70	1192	16.79 ± 0.48
	M	adult	14030942	PTT	37389	5/1/06	66	1006	15.01 ± 0.7
	M	adult	14052375	PTT	37629	15/2/06	107	1001	9.62 ± 0.38
	F	adult	14049642	PTT	37631	21/2/06	135	1275	9.73 ± 0.29
		juvenile	14052638	PTT	55167	14/12/04	60	145	2.38 ± 0.14
		juvenile	14052370	PTT	55166	14/12/04	97	225	2.34 ± 0.09

* One grey-headed albatross (A0409) was tracked twice.

Table S2 Source of environmental and atmospheric data used to predict foraging effort.

Acronym	Data	Justification for proxy	Temporal resolution	Dataset	Source
chl	Chlorophyll a concentration	Regions of high productivity	monthly	Ocean data MODIS Aqua Level-3 binned daily remote sensing reflectance	http://oceancolor.gsfc.nasa.gov/
eke	Eddy kinetic energy	Eddy features that may concentrate productivity	daily	SSALTO/DUACS gridded absolute geostrophic velocities	http://www.aviso.altimetry.fr/en/data/products/sea-surface-height-products/global/msla.html
bathy	Bathymetry gradient	Bathymetric features e.g. shelf, sea mounts; that may cause upwelling and elevate surface productivity	NA	ETOPO2	http://www.ngdc.noaa.gov/mgg/global/etopo2.html
gsst	Sea surface temperature gradient	Frontal zones that may concentrate productivity	daily	NOAA Optimum Interpolation Sea Surface Temperature V2	http://www.esrl.noaa.gov/psd/data/gridded/data.noaa.oisst.v2.html
ssha	Sea surface height anomaly	Eddy features that may concentrate productivity	monthly	SSALTO/DUACS gridded mean and climatological sea level anomalies	http://www.aviso.altimetry.fr/en/data/products/sea-surface-height-products/global/msla-mean-climatology.html
wind	Surface wind speeds	Areas with high wind driven mixing and productivity; and an influence on albatross flight costs	twice daily	NCEP-DOE Reanalysis 2 daily averages	http://www.esrl.noaa.gov/psd/data/gridded/data.ncep.reanalysis2.html

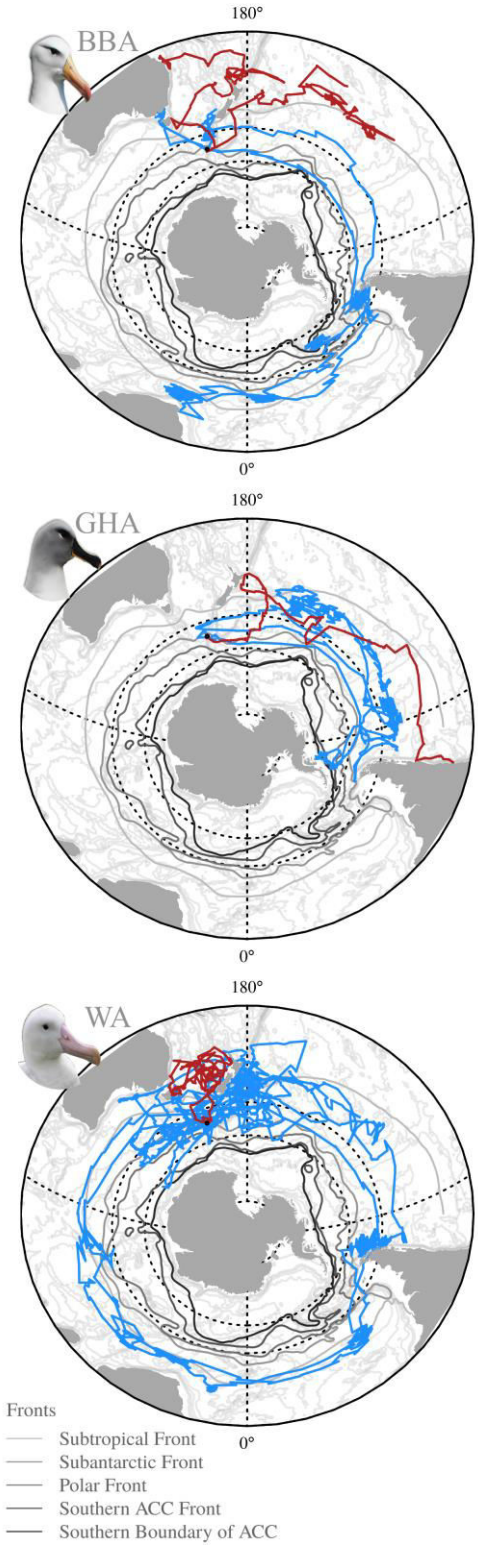

Figure S1 Individual tracks from juvenile (red) and nonbreeding adult (blue) black-browed (BBA, n = 2, 2), grey-headed (GHA, n = 2, 2), and wandering (WA, n = 2, 5) albatrosses tracked from Macquarie Island in relation to major oceanic fronts from Orsi *et al.* 1995.

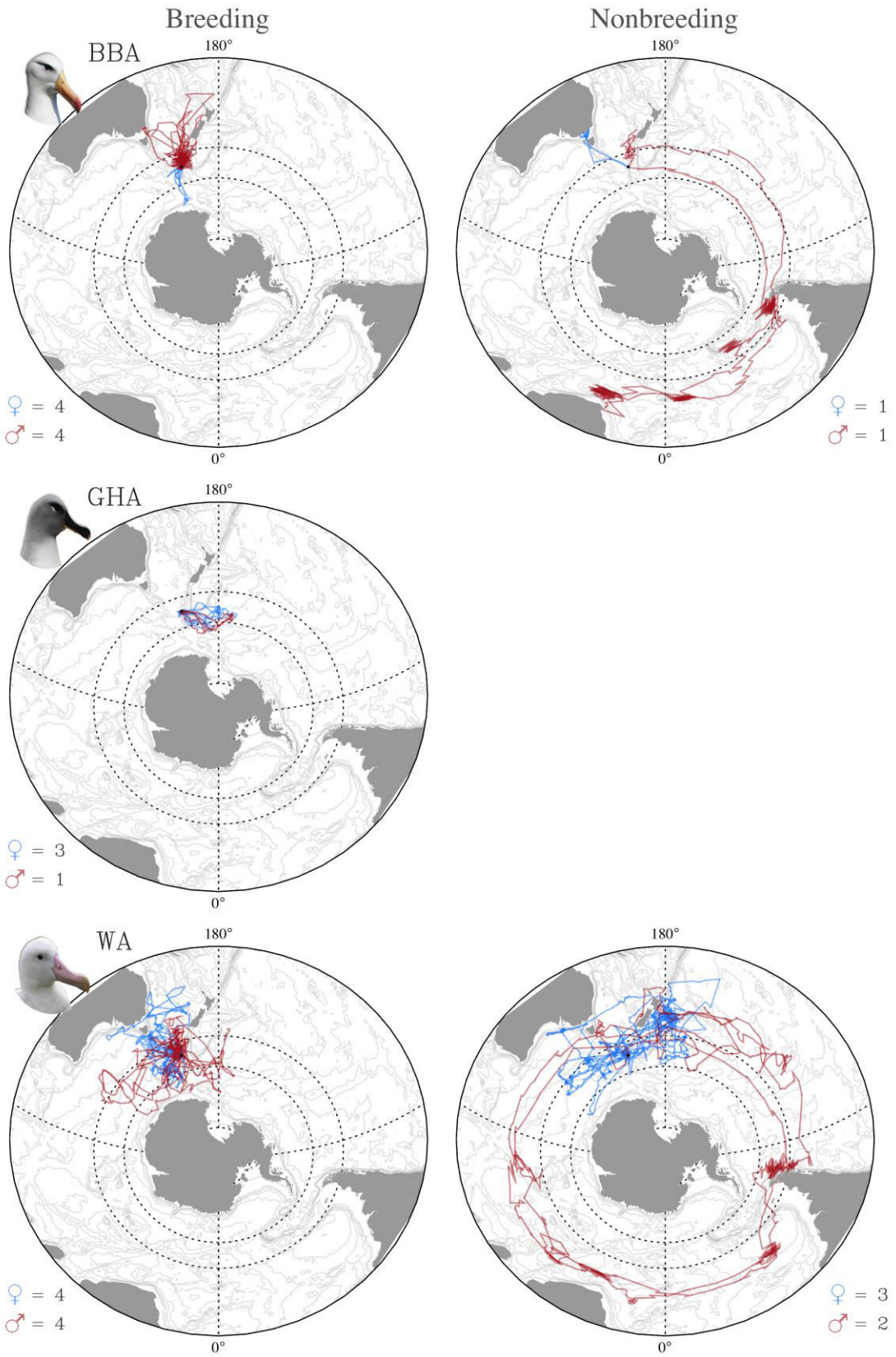

Figure S2 Individual tracks from breeding and nonbreeding black-browed (BBA), grey-headed (GHA) and wandering albatrosses (WA) of known sex tracked from Macquarie Island.

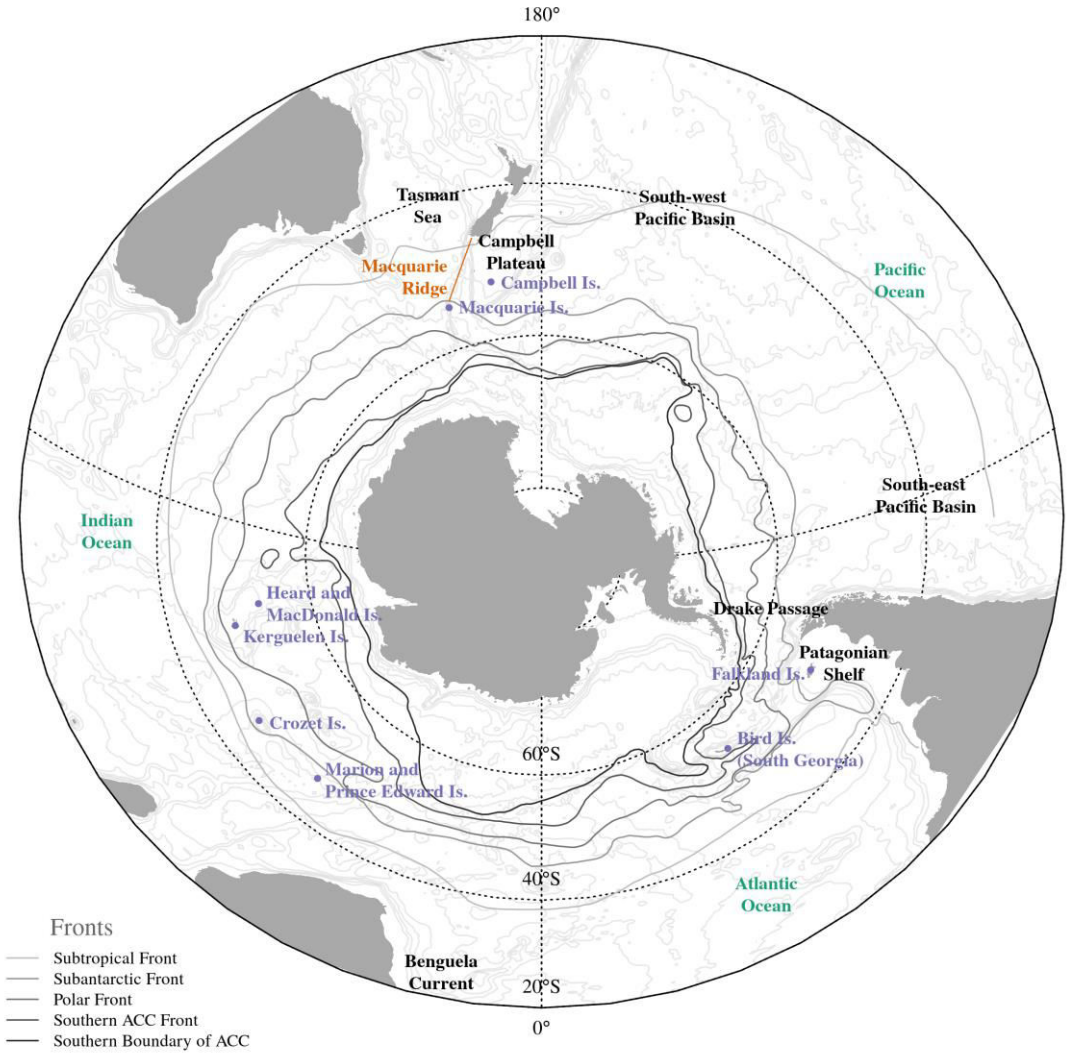

Figure S3 Subantarctic islands and important Southern Ocean features for Macquarie Island albatrosses including major oceanic fronts from Orsi *et al.* 1995.

Chapter 3

Introduced rabbits and extreme weather events: a dangerous combination for the reproductive output of three sympatric albatrosses

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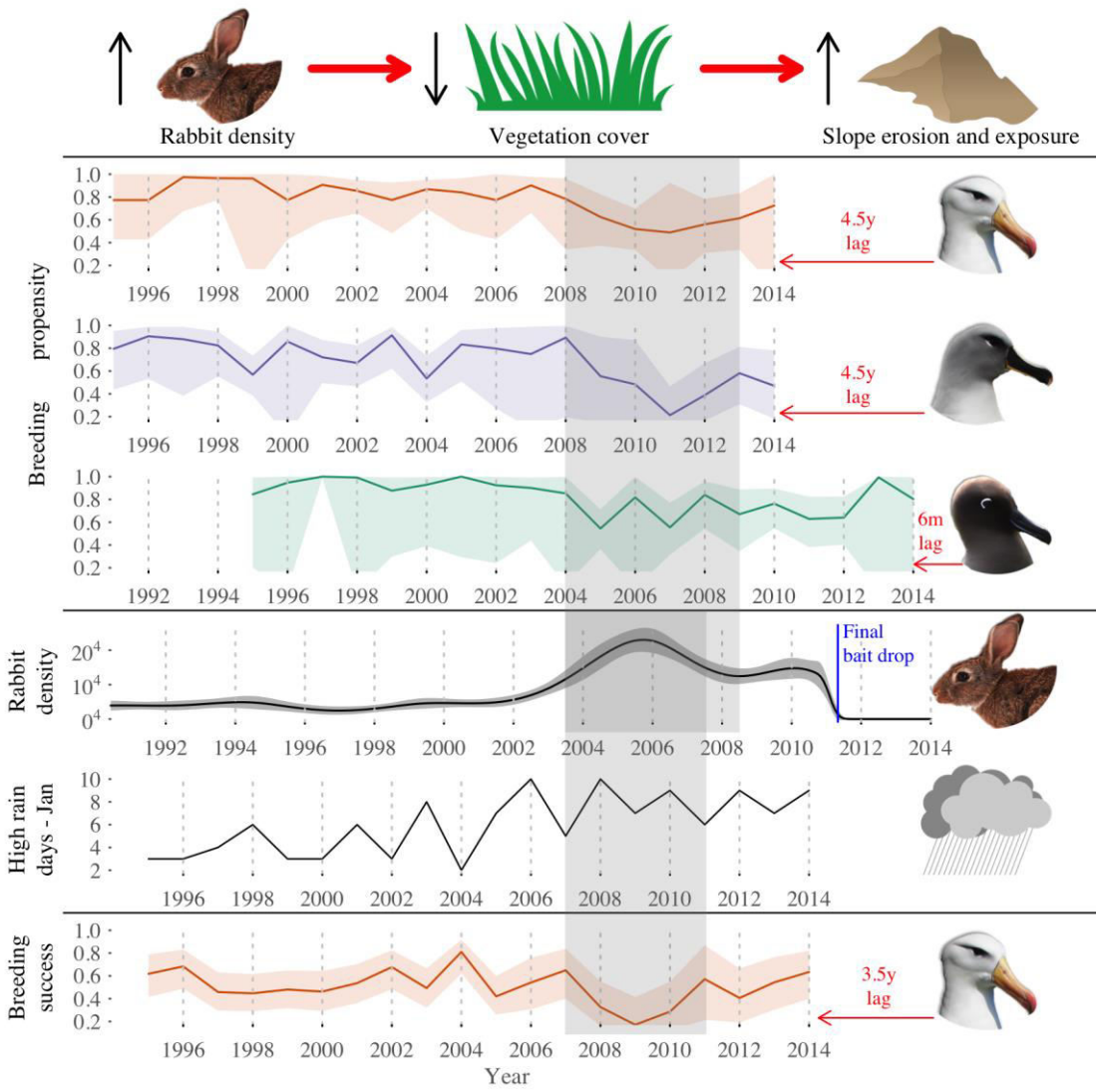
Abstract

Invasive species present a major conservation threat globally and nowhere are their impacts more pronounced than in island ecosystems. Determining how native populations respond demographically to invasive species can provide information to mitigate the negative effects of invasive species. Using 20 years of mark-recapture data from three sympatric species of albatrosses (black-browed *Thalassarche melanophris*, grey-headed *T. chrystostoma*, and light-mantled albatrosses *Phoebetria palpebrata*), I quantified the influence of invasive European rabbits *Oryctolagus cuniculus* and extreme weather patterns on breeding propensity and success. Temporal variability in rabbit density explained 20-76% of the variability in breeding propensity for all three species, with severe decreases in breeding propensity observed during periods of highest rabbit numbers. For black-browed albatrosses, the combination of extreme rainfall and high rabbit density explained 50% of total trait variability and dramatically reduced breeding success. I showed clearly that invasive rabbits and extreme weather events reduce reproductive output in albatrosses and that eliminating rabbits had a positive effect on albatross reproduction. This illustrates how active animal management at a local breeding site can result in positive population outcomes even for wide ranging animals like albatrosses where there is little capacity to influence vital rates during their at-sea migrations.



Graphical abstract Breeding propensity and breeding success probabilities of adult black-browed (orange), grey-headed (purple) and light-mantled albatrosses (green) in relation to high densities of invasive rabbits and climate driven extreme rainfall events at subantarctic Macquarie Island. Spatial heterogeneity in rabbit grazing and albatross nest sites explains the delayed response of individual albatross species to heavy grazing and subsequent slope erosion.

Introduction

Invasive species are a major threat to global biodiversity, with the capacity to cause rapid ecosystem change (Vitousek et al., 1996, Bergstrom et al., 2009). Island ecosystems, which generally show high levels of endemism, are particularly vulnerable to the direct and indirect stressors of invasive species, including competition, predation and habitat degradation (Berglund et al., 2009). The influence of invasive species on island ecosystems already experiencing pressure from global climate change may result in trophic imbalances amongst native communities, and reduced species resilience in the face of multiple threats (Smith and Steenkamp, 1990). Further, given the frequency and severity of extreme weather events, such as heat waves and precipitation, are predicted to increase as a result of global climate change (IPCC, 2012), their effects on island ecosystem structure and function are likely to be exacerbated (Bergstrom et al., 2015). In severe cases, the combination of invasive species and extreme weather events could have particularly serious demographic consequences for threatened native species.

Amongst invasive species, introduced mammals are particularly problematic (Courchamp et al., 2003). The defining characteristics of the most successful mammalian invaders are high adaptability and rapid reproduction, both of which increase the likelihood of population establishment and the rate of dispersal (Capellini et al., 2015). The European rabbit *Oryctolagus cuniculus* epitomises these life history traits, contributing to its historical dominance as a successful invasive species worldwide (Flux and Fullagar, 1992). Acting as an ecosystem engineer, rabbits can reduce landscape heterogeneity through over-grazing that can lead to catastrophic habitat degradation (Selkirk et al., 1983). Rabbit populations typically grow quickly before decreasing rapidly once local carrying capacity is reached in a boom and bust scenario (De Villiers et al., 2010, Terauds et al., 2014). The transitional period between the boom and the bust can rapidly transform a landscape through high vegetation suppression and increased erosion rates and consequently, drastically degrade native species communities (Scott and Kirkpatrick, 2008, 2013).

Invasive rabbits on islands often co-exist with native seabird colonies (Weimerskirch et al., 1989, McChesney and Tershy, 1998), with vegetation providing fodder for rabbits and nesting habitat for seabirds. There are profound demographic responses of burrowing seabirds to high rabbit density, including reduced reproductive output through increased competition for burrow-nesting habitat (Brothers and Bone, 2008, Brodier et al., 2011).

However, for surface-nesting seabirds such as albatrosses, the consequences of high rabbit density and associated habitat change are unknown. As rabbit population densities grow, elevated grazing pressure leads to a reduction in vegetation cover and plant diversity (Mutze et al., 2016), with the potential to deplete available nesting material, increase predation risk, or increase variability in nest microclimate. Surface-nesting seabirds that are more exposed to weather conditions may face greater energetic costs of incubation or brooding, and unattended chicks may have higher thermoregulatory costs (Kim and Monaghan, 2005, D'Alba et al., 2009). With greater exposure, the risk of predation is also likely to increase, as adults, eggs and chicks become more visible (Colchero et al., 2010). At high rabbit densities, increased soil erosion rates driven by severe vegetation suppression may influence nest site selection, as some areas become less suitable (Scott and Kirkpatrick, 2008).

Subantarctic Macquarie Island has experienced drastic change over the last ~140 years due to the establishment and proliferation of invasive species. First introduced by pre-industrial commercial sealers in the late 19th century; cat *Felis catus*, weka *Gallirallus australis scotti*, rabbit, rat *Rattus rattus* and mouse *Mus musculus* populations have fluctuated due to variability in resource availability and more recently through management interventions (Copson and Whinam, 2001, Raymond et al., 2011). With coordinated releases of the rabbit control virus Myxoma, rabbit numbers were reduced from around 300,000 in 1977 to 30,000 or less by the late 1980s, remaining low until the late 1990s (Terauds et al., 2014). A subsequent rapid rise in rabbit numbers between 2001 and 2005 has been attributed to multiple factors including the eradication of feral cats, reduced distribution and effectiveness of the Myxoma virus, warmer climatic conditions and increased availability of food resources as a result of 20 years of vegetation recovery following a myxo-induced reduction of the rabbit population (Bergstrom et al., 2009, Dowding et al., 2009, Whinam et al., 2014). Before they were eradicated in 2000, feral cats preyed heavily on rabbits and burrowing petrels, using both as a main prey source (Jones, 1977, Brothers and Bone, 2008). However, there are no reliable indications that cats regularly preyed upon nesting albatrosses, possibly due a surplus of preferred prey and an effective defence mechanism: the regurgitation of stomach oil (Jones, 1977). In 2014, one of the largest and most ambitious invasive species eradications to date was deemed successful in removing rabbits, rats and mice from Macquarie Island (Springer, 2016). While present on the island, rabbits caused widespread and severe vegetation suppression, enhanced slope erosion and more frequent landslide events (Fig. S1 & Fig. S2) (Scott and Kirkpatrick, 2008, 2013). Spatial and temporal patterns in rabbit

density and subsequent habitat degradation were not uniform across the island. Patterns in rabbit density show numbers reaching a peak in smaller, localised areas before declining, representing the carrying capacity of the area and depletion of available food (Terauds et al., 2014). The peak in rabbit density in the north of Macquarie Island (2005) occurred approximately four to five years prior to the peak in the middle and south of the island (2009) (Terauds et al., 2014). Furthermore, rabbit impacts have coincided with changes in climate: increases in surface air temperatures by 0.62°C (1948-2007), total annual precipitation by 35%, and higher wind speeds (Adams, 2009, Hande et al., 2012, Hindell et al., 2012). Increasing annual rainfall has the capacity to increase the frequency and extent of landslips, and the rate of erosion rates on Macquarie Island's coastal slopes, made worse in recent years by the widespread loss of vegetation from rabbit grazing (Scott and Kirkpatrick, 2008).

Four species of albatrosses breed on Macquarie Island, of which three; black-browed *Thalassarche melanophris*, grey-headed *T. chrysostoma* and light-mantled albatrosses *Phoebetria palpebratra* nest on high, exposed nest sites. These steep escarpments have experienced major degradation driven by over-grazing and landslips from resulting soil instability, geological activity and heavy rainfall events (Fig. 1) (Kim and Monaghan, 2005). Quantifying the progressive influence of invasive species on the demographic rates of native island species is often hampered by the lack of available data on invasive species populations. Additionally, understanding the medium to long-term demographic effect of extreme weather conditions requires long-term biological datasets. Together, these challenges mean that few studies have addressed the synergistic effects of both invasive species and weather.

Figure 1 Photos illustrating nest exposure and microclimate differences of a) a pre-fledging light-mantled albatross chick nesting in a region of Macquarie Island protected by a rabbit-proof fence (date taken: 2006-04-11) compared to b) a well-grown chick in a heavily rabbit-grazed region in the south-east of Macquarie Island (date taken: 2007-02-24).

I quantified the influences of rabbit density and extreme weather conditions on the breeding propensity and breeding success of these three albatross species. Understanding the influence of these factors may provide insights into population dynamics of albatross populations and provide a basis for assessing the implications of active management at colonies, such as the eradication of invasive vertebrates.

Methods

I used 20 years (1995-2014) of capture-mark-recapture data in a multi-event modelling approach from three albatross species breeding on Macquarie Island (54.6° S, 158.9° E) to quantify the influence of invasive rabbits and weather patterns on albatross breeding propensity and breeding success.

Field methods

Macquarie Island is a narrow, elongated, uplifted island oriented approximately north-south. The coastal perimeter of the island rises steeply from sea level to approximately 300 m and provides habitat for escarpment-nesting albatrosses. Albatross construct their nest using nearby material, such as mud, vegetation and other natural debris shaped into a pillar with a

rounded hollow on the top that forms the nesting bowl. Adults continue to maintain the nest throughout incubation by adding more organic material.

Between 1995 and 2014 (seasons 1994/95 and 2013/14), all accessible albatross chicks at one black-browed, one grey-headed (encompassing the entire island breeding populations) and seven light-mantled albatross study sites (~10% of total island breeding population) were banded with stainless steel bands. The majority of breeding adults had existing bands from previous long-term studies. Over the study period, annual nest visits during incubation allowed the bands of breeding adults and the presence of an egg to be recorded. Banded nonbreeding adults observed within the study site were also recorded and cross-referenced against observed breeding adults to ensure accurate recording of breeding status. Breeding propensity was estimated as the probability that a mature female attempts to breed in a given year. Nest checks at the end of the breeding season determined whether the chick fledged successfully as a measure of breeding success.

A geographic survey was undertaken in the 2013/14 season to establish physical differences in elevation, slope angle and aspect of nests of the three species (black-browed, n = 44, grey-headed, n = 87, and light-mantled albatrosses, n = 234). Elevation was measured using a calibrated Garmin GPSMAP 64s with a built-in barometric altimeter. A Suunto PM-5/360 PC Clinometer was used to determine the slope angle of the escarpment at the nest site. A bearing measurement taken approximately 90° perpendicular to the slope at the nest site using a handheld compass was used to determine nest aspect. Differences in nest site characteristics (aspect, elevation and slope angle) among species were tested using one-way ANOVA and Tukey's HSD test.

Reproductive output analysis

An encounter history was produced for each individual (black-browed, n = 225; grey-headed, n = 513; and light-mantled albatrosses, n = 1215) which included several observable adult states, successful breeder (coded 1), failed breeder (coded 2), nonbreeder (coded 3); and unobservable states (coded 0) corresponding to post-successful breeder, post-failed breeder and post nonbreeder (Appendix S1). Unobservable states were included in the analyses to account for the biennial breeding behaviour of grey-headed and light-mantled albatrosses, which results in year-to-year differences in the transitional breeding propensity (ψ); the probability of an individual breeding the year following a successful breeding attempt is low,

higher after a failed attempt and greatest after a nonbreeding season (Fig. S3a) (Barbraud and Weimerskirch, 2012). All chick, juvenile and nonbreeding states before the first breeding attempt were suppressed to focus on reproductive parameters.

Due to the timing of the field seasons, some nests were not revisited late in the season, and this uncertainty in breeding outcome (coded 4) was incorporated in an event matrix (Gimenez et al., 2012), representing 1.5%, 1.1% and 1.3% of observations for black-browed, grey-headed and light-mantled albatrosses, respectively.

To test for goodness-of-fit, encounter histories were transformed to single-state and assessed using U-Care 2.3.2 software, including tests for transience (Pradel et al., 2005, Choquet et al., 2009a). Tests for trap-dependence (Test 2: 2.CT + 2.Cl) were excluded since the model structure accounted for differences in breeding propensity based on previous breeding states, characteristic of skip-breeding (Barbraud and Weimerskirch, 2012). A correction for lack of fit within the populations was applied using an over-dispersion factor (ĉ) (Lebreton et al., 1992).

Over the study period, rabbit-driven changes in breeding habitat condition influenced nest accessibility for investigators. Changes in detection probability (p) were therefore quantified and incorporated in the demographic models (see Fig. S4). The influence of rabbits on detection was addressed by including rabbit density as a covariate on modelled detection probability (Table S1). Detection probabilities were estimated separately for breeders and nonbreeders, as bands are harder to read on non-nesting birds.

Adult survival (Φ), return rates (r), breeding propensity (β), breeding success (γ), and detection probability (P) were estimated using E-Surge 1.9.0 software (Choquet et al., 2009b). See Fig. S3b for probability estimation schematic, Appendix S2 for transition matrix structure and Table S1 for input notation. For black-browed albatrosses, the breeding propensity (β) and breeding success (γ) estimates were derived using a time-dependent (t) model for all adult observable states due to their annual breeding behaviour. Given the difference in likelihood of carry-over effects on the current state from the previous state of biennial breeders, the probability of return and breeding for successful breeders was different to failed and nonbreeders for the original time-dependent models, except when modelling the

demographic parameter of interest, where time-dependent parameters were retained. This constituted our general model for grey-headed and light-mantled albatrosses.

Demographic model selection was based on Akaike's information criterion (AIC), whereby the model with the lowest AIC (ΔQAIC > 2) was chosen as the best model (Burnham and Anderson, 2002). The most parsimonious model was chosen where ΔQAIC < 2. While it was necessary to address time-dependent variation in adult survival and return probabilities to evaluate reproductive parameters accurately, further interpretation of these is outside the scope of this chapter (see Chapter 4), which is focused on breeding propensity and success.

Environmental covariates

Environmental covariates were included in the demographic modelling to quantify the influence of rabbit density and extreme weather events on breeding propensity and breeding success. Monthly estimates of island-wide rabbit density (*i.e.* one value for the entire island for each month from 1994 to 2014) were taken from Terauds et al. (2014), who used a smoothed regression model to generate island-wide estimates from rabbit counts in two-hectare study plots. Analyses of breeding propensity used averaged monthly rabbit densities during the preceding nonbreeding period, and of breeding success analyses included averaged monthly densities in the corresponding breeding season. It is known that rabbit density was not spatially uniform across the island. High rabbit density regions shifted over the study period resulting in localised patches of severe grazing (Scott and Kirkpatrick, 2013). The region-specific rabbit density data represents individual count data, which shows large inter-annual and intra-annual fluctuations and may obscure any important relationship between albatross breeding. Therefore, modelled island-wide estimates from Terauds et al. (2014) were implemented in the demographic modeling because of the extensive effort this study takes to ensure data accuracy and completeness across the time-series that aligns with the albatross demographic dataset used in this chapter. Light-mantled albatrosses breed widely across the island whereas breeding colonies of black-browed and grey-headed albatrosses are restricted to the southern end of the island, and so rabbit impacts were not expected to be synchronous between the three species. Furthermore, the impact of high rabbit density is primarily through overgrazing of vegetation, causing direct changes to habitat and subsequent loss of soil stability. These effects occur over variable time scales, and so I used biannual lags (from 0 - 5 years) on predictor variables in the models. These lags reflect not only the duration between high rabbit density, vegetation suppression and slope erosion, but also

spatio-temporal patterns in grazing. Peaks in rabbit density at the southern extent of the island, where the black-browed and grey-headed albatrosses nest, occurred approximately four years later than the peak in island-wide rabbit density and had a more substantial affect on slope stability (Fig. S5) (Terauds et al., 2014).

To investigate the influence of extreme events on breeding success during the early chick-rearing period, when chicks are most vulnerable and thermoregulatory costs are high (Visser, 1998), I included heavy rainfall events in the modelling. January daily rainfall (mm) values obtained from the Bureau of Meteorology weather station on Macquarie Island were summarised into the number of days above the 80th percentile of the study period average and included as a covariate to capture the frequency of extreme rainfall events. This equated to the number of January days with total rainfall above 4.40 mm.

The significance of each covariate on modelled breeding propensity and breeding success was assessed using ANODEV, and the magnitude of its effect determined according to both the total variation explained by the covariates (R^2) and the total variation explained by the covariates when temporal trends have been removed from the variable and the demographic rate (de-trended R^2) following Grosbois et al. (2008). The de-trended models provided a short-term measure of variation compared to the standard models, which consider long-term variability and can be sensitive to temporal trends in the environmental covariate and demographic rate.

Results

Model parameters

Poor model fit was found for all three species; black-browed ($\chi^2_{95} = 154.15$, $p < 0.001$), grey-headed ($\chi^2_{124} = 390.28$, $p < 0.001$) and light-mantled albatrosses ($\chi^2_{219} = 799.70$, $p < 0.001$). For grey-headed and light-mantled albatrosses trap-shyness was detected ($\chi^2_{21} = 221.47$, $z = 10.22$, $p < 0.001$ and $\chi^2_{29} = 381.08$, $z = 15.31$, $p < 0.001$, respectively), i.e., where individuals encountered on the first occasion tend to be encountered less at the second occasion. The biennial breeding frequency and associated lower breeding propensity of grey-headed and light-mantled albatrosses may explain the trap-shyness detected for these species. Biennial breeding is accounted for in the mark-recapture modelling by possible transitions into unobservable states. In contrast, trap-happiness was detected for black-browed albatrosses ($\chi^2_{23} = 88.29$, $z = -6.30$, $p < 0.001$). Trap-happiness, in this case, appears to be an

artefact of reduced accessibility for investigators to portions of the study site during periods of high rabbit grazing; consequently, individuals in accessible locations were reencountered more frequently. Black-browed albatross encounter histories showed evidence of underdispersion. The biological explanation for underdispersion is unclear and may simply reflect greater uncertainty in the estimation process due to a smaller sample size. To correct for lack of fit to the underlying capture-mark-recapture assumptions, over dispersion factors ($\hat{c}$) of 0.71, 1.00 and 1.46 were included in the models for black-browed, grey-headed and light-mantled albatrosses, respectively (Barbraud and Weimerskirch, 2012).

Temporal trends in reproductive rates

Breeding propensity (β) of both black-browed and grey-headed albatrosses decreased over the study period (1995-2014) (Fig. 2a-b & Table S2). Although there was a considerable reduction in mean breeding propensity between 1995-2004 (mean: 0.93 ± 0.02) and 2005-2014 (mean: 0.73 ± 0.04) of light-mantled albatrosses, a significant trend was not detected, presumably due to high inter-annual variability (Fig. 2c). No trends were detected in breeding success of any species across the study period (Table S2).

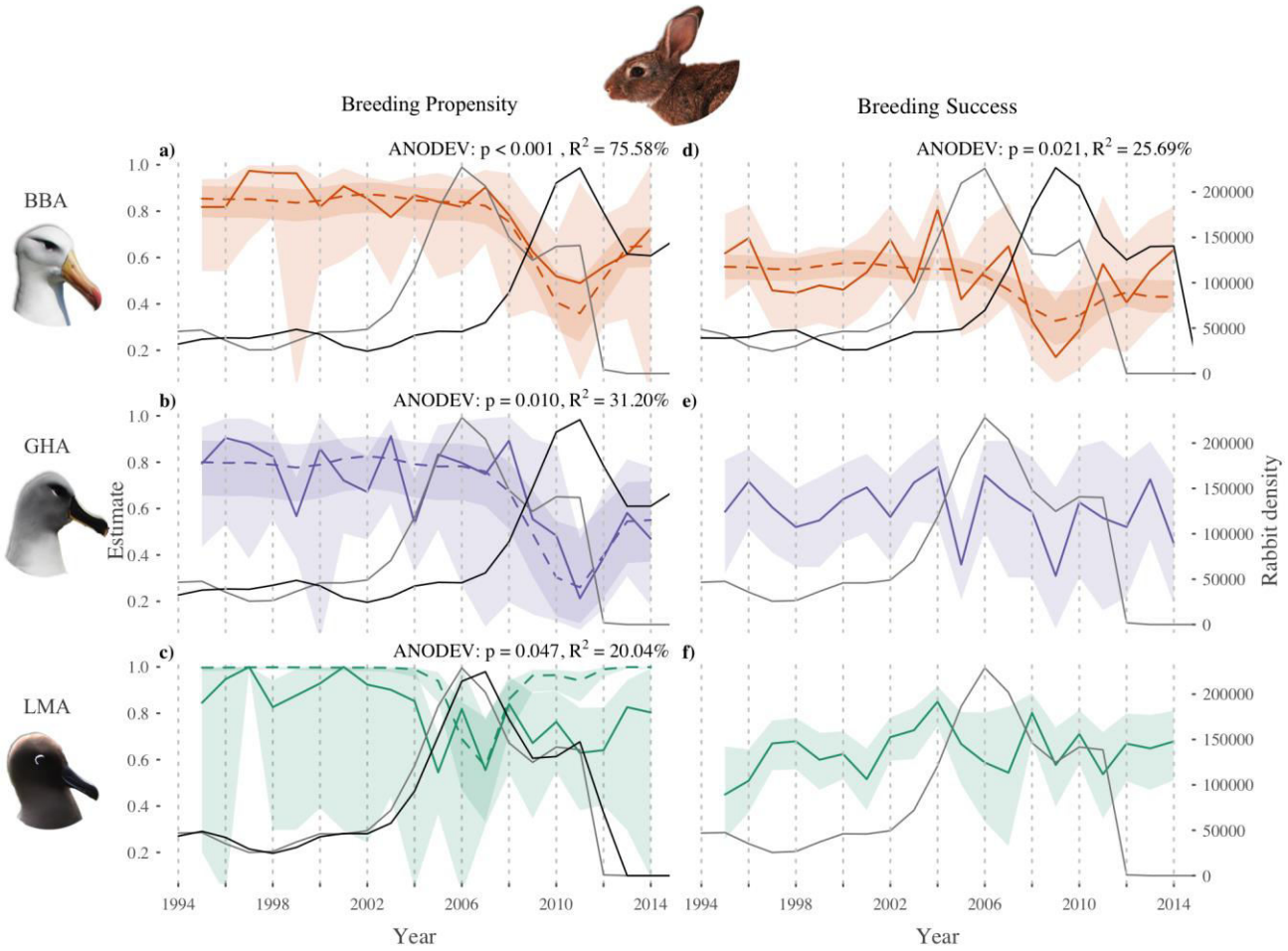


Figure 2 Annual variation in adult breeding propensity (a-c) and breeding success (e-f) of albatrosses at Macquarie Island (black-browed, BBA; grey-headed, GHA; and light-mantled albatrosses, LMA), modelled as time-dependent rates (solid coloured lines) and as a function of the covariate (including 0.95 confidence intervals), lagged island-wide rabbit density (broken coloured lines), overlaid with raw island-wide rabbit density data from Terauds *et al*. 2014 (raw data, grey solid lines and lagged, black solid lines).

Effects of high rabbit density on reproductive parameters

High island-wide rabbit density was associated with decreases in breeding propensity of all three species, explaining 75.6%, 31.2% and 20.1% of the variance for black-browed, grey-headed and light-mantled albatrosses, respectively (Fig. 2a-c). I found substantial lags between increases in rabbit density and decreases in reproductive output, which were not consistent across species. Light-mantled albatrosses, which breed island-wide, showed decreases six months after high rabbit density. Black-browed and grey-headed albatrosses, which only breed at the southern end of the island, showed a four and a half-year lag between high rabbit density and low breeding propensity. When rabbit density (lagged) was highest, the modelled breeding propensity of black-browed, grey-headed and light-mantled albatrosses decreased by 36.7%, 73.2%, and 34.3%, respectively from the beginning of the study. Following the peak in rabbit density, the subsequent decrease associated with the pest eradication corresponds with a restoration in breeding propensity by 48.0%, 120.6% and 44.8% for black-browed, grey-headed and light-mantled albatrosses, respectively.

A negative correlation between rabbit density and breeding success was detected for black-browed albatrosses, explaining 25.7% of the variance of modelled breeding success, and showing the lowest estimate (0.17±0.09) 3.5 years after peak rabbit density (Fig. 2d). This corresponded with a decrease of 72.4% in modelled breeding success from the beginning of the study. In parallel with the decrease in rabbit density was a concurrent increase in black-browed albatross breeding success by 271.6%. There was no effect of rabbit density on breeding success of grey-headed and light-mantled albatrosses (Fig. 2e-f).

Effects of climatic conditions on reproductive output

The relationship between extreme rainfall on breeding success was only obvious for black-browed albatrosses, explaining 28.2% of the variation (Fig. 3a-b). The total percentage of temporal variance in breeding success explained by rabbit and rainfall variables combined was 49.6% (Fig. 3b).

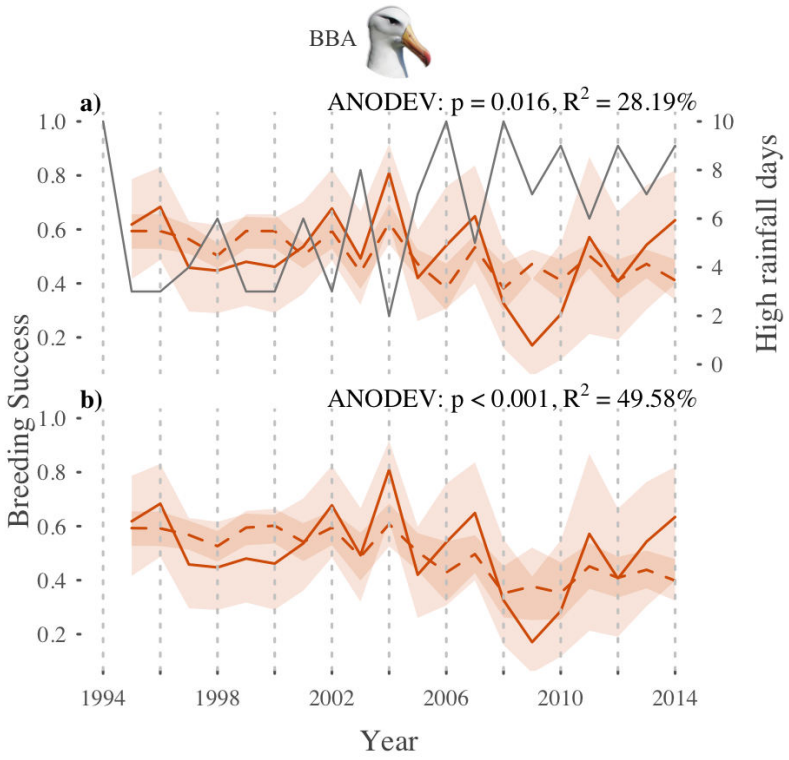


Figure 3 Annual variation in breeding success probabilities of adult black-browed albatrosses (BBA) at Macquarie Island, modelled as time-dependent breeding success (solid coloured lines) and as a function of the covariates (broken coloured lines, including 0.95 confidence intervals), a) number of January days with total rainfall in the 80th percentile (1995-2014, grey solid lines) and b) combined island habitat model including aforementioned rain covariate and island-wide rabbit density from Terauds et al. (2014).

Nest site characteristics

There were differences in nest site characteristics among the three albatross species; black-browed albatrosses showed a preference for low elevations (n = 44, $\bar{x}$ = 52.7 ± 5.1 m above sea level) and low slope angles (n = 44, $\bar{x}$ = 44.1± 2.4°), and grey-headed albatrosses for high elevations (n = 87, $\bar{x}$ = 99.6 ± 2.9 m above sea level) and high slope angles (n = 87, $\bar{x}$ = 49.9 ± 1.4°), whereas light-mantled albatrosses showed more variability in elevation (n = 234, $\bar{x}$ = 76.0 ± 2.4 m above sea level) and slope angle (n = 234, $\bar{x}$ = 43.6 ± 0.9°) (Fig. 4a-b). These species-specific differences in nest aspect were, in general, related to the topography of Macquarie Island and colony location (F_2 = 140.6, p < 0.001) (Fig. 4c). Colonies of black-browed and grey-headed albatrosses had south-easterly (n = 44, $\bar{x}$ = 159.3 ± 0.1°) and southerly (n = 87, $\bar{x}$ = 176.9± 0.1°) nest aspects, respectively, reflecting the typical slope aspect at the southern extent of the island. In contrast, light-mantled albatrosses had a broad, island-wide nesting distribution, with the highest concentrations on the east coast where six of seven study sites are located, reflected in the observed nest aspects (n = 234, $\bar{x}$ = 70.3 ± 0.1°). All means are presented with standard error of the mean.

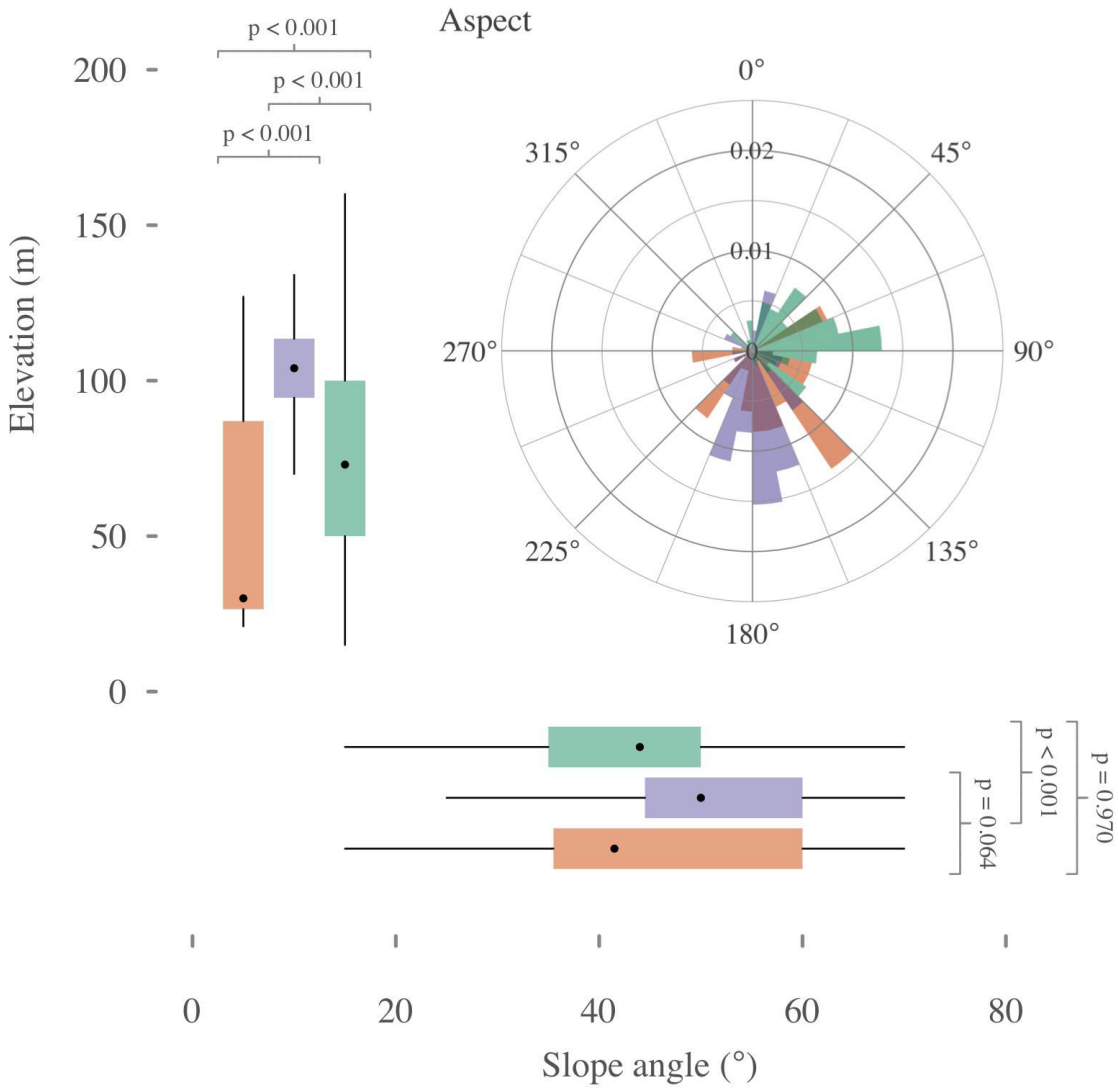


Figure 4 Observed differences in nest site characteristics of albatrosses at Macquarie Island (black-browed, orange; grey-headed, purple; and light-mantled albatrosses, green) including a) elevation (metres above sea level) b) slope angle and c) nest aspect. The boxplot range reflects 95% CI of the mean and whiskers are 1.5 times the IQR.

Discussion

With a rare insight into the long-term population fluctuations of an invasive species prior to successful eradication I described for the first time the relationship between rabbit grazing and the reproductive output of a threatened albatross community.

Impact of high rabbit density on albatross reproductive output

At the community level, rabbit density explained a significant proportion of the temporal variation in the reproductive output of the albatross community with reproductive output

lowest when the impact of high rabbit density on vegetation and habitat quality was the greatest. Rarely have such colony-based drivers of seabird breeding propensity been quantified or shown to explain trait variation for a community of species. Our findings offer compelling support for management intervention, in this case the large-scale eradication of rabbits, which appears to have provided major conservation benefits, including a potential increase in reproductive output for an endangered community of albatrosses.

I suggest that the cascading effects of high rabbit density on albatross reproductive output occurred via two, sequential, mechanisms: i) vegetation degradation directly affecting nest site habitat and microclimate over short temporal scales, and ii) vegetation degradation and rabbit burrowing activity reducing soil stability and amplifying natural erosion rates, leading to large-scale degradation of overall slope integrity reduced habitat suitability at breeding colonies.

The greater affect of habitat degradation on breeding propensity rather than breeding success is unexpected given that albatross are found breeding in exposed colonies with very little vegetation cover (e.g. Steeple Jason Island black-browed albatross colony and The Mewstone shy albatross *Thalassarche cauta* colony). Regardless, albatrosses on Macquarie Island bred in areas of dense tussock grass (*P. foliosa* and *P. cookii*) during periods of effective rabbit control, until management intervention ceased and heavy rabbit grazing transformed the landscape. Founding nest site selection is likely to be strongly influenced by habitat quality, which for Macquarie Island albatross was drastically and rapidly reduced to dead tussock pedestals, bare ground and mud following increased rabbit numbers. Habitats that provide protection from adverse weather conditions, reduced variability in nest microclimate and cover from predators would, in theory, be selected preferentially (Stenhouse and Montevecchi, 2000). As adults return to colony, and encounter poor nesting conditions, they may either invest in breeding in substandard conditions or skip breeding, consequently maintaining body condition until nest site conditions improve. For Macquarie Island albatrosses, reduced breeding propensity during periods of severe rabbit damage potentially reflects their adaptive capacity, whereby the energetic costs of breeding are avoided when the likelihood of reproductive success is low. As long-lived species, albatrosses have many opportunities to breed and can skip some breeding opportunities with little consequence for individual fitness and lifetime fecundity (Dobson and Jouventin, 2010). However, continuous

skipping and low breeding propensity can have delayed population level consequences by reducing breeding population recruitment rates.

Lower breeding propensity may also be influenced by the functional role of vegetation as nesting material. From vegetation photo monitoring of the black-browed and grey-headed albatrosses slopes on Macquarie Island a rabbit driven transition from dominant tall tussock (*Poa foliosa* and *Poa cookii*) and mega-herb species (*Stilbocarpa polaris*) to bare ground and secondary succession of *Leptinella plumosa* has led to an overall reduction in the availability and quality of nesting material (Fig. S2). Lack of material potentially increases the energetic cost of nest building, reduces the quality of nests and, in extreme cases, may disrupt courting behaviour, formation of new partnerships, or the likelihood of laying.

The negative relationship between rabbit density and breeding success of black-browed albatrosses may reflect an increase in the metabolic cost of incubation and brood for adults due to reduced vegetative cover and the increased exposure to wind and rain preventing efficient thermoregulation by chicks (Bakken et al., 2002, Pistorius et al., 2015, Høyvik Hilde et al., 2016). Furthermore, the loss of nesting habitat through grazing introduces greater variability in microclimate around the nest, and both adult and chick are then more exposed (Fig. 1). A decline in nest quality and slumping associated with reduced availability of nesting material may also explain reduced breeding success. At the Chatham Islands, storm-driven reductions in soil and vegetation from several breeding sites of Chatham (*Thalassarche eremita*) and Northern Royal (*Diomedea sanfordi)* albatrosses has resulted in a considerable decline in hatching success (Gales and Robertson, 1998). Furthermore, the loss of vegetation cover might also have led to increased predation on chicks from brown skuas (*Catharacta antarcticus*) and giant petrels (*Macronectes* sp.) (Raymond et al., 2011). Rabbit densities, vegetation suppression and predation risk impact chick survival through a complex interplay of processes. The eradication of rabbits and subsequent drop in grazing pressure has allowed the vegetation to recover, but also potentially increased predation risk, as skuas lose rabbits as a principal prey resource (Raymond et al., 2011). The significant correlation between rabbit density and breeding success in black-browed, but not in grey-headed or light-mantled albatrosses, may also be related to the annual breeding strategy of black-browed albatrosses. As annual breeders, black-browed albatrosses face a greater number of years of poor slope condition over the study period. Alternatively, black-browed nests on Macquarie

Island predominantly face south-east into the prevailing winds, which may increase the vulnerability of chicks to storm events when vegetation cover is poor.

Delayed effects of high rabbit density

The asynchronous relationship between breeding propensity and rabbit density reflects spatio-temporal heterogeneity in grazing pressure. Prior to this study, the rabbit population on the island was estimated to be several hundred thousand individuals in the mid-1970s, before it was reduced to just tens of thousands around 1997 (Terauds et al., 2014). Following the introduction of myxomatosis in 1978, rabbit numbers plummeted and remained low until the mid-1990s (Brothers et al., 1982, Terauds et al., 2014). Rabbit numbers increased dramatically from 1998 to 2006 (Terauds et al., 2014) and this boom in rabbit numbers coincided with our study period. This increase reflects growth of localised rabbit populations, particularly in the south of the island, which represents black-browed and grey-headed nesting sites, and at the time showed greater vegetation diversity and abundance (Scott and Kirkpatrick, 2013). By 2008, heavy grazing had resulted in severe vegetation suppression and slope degradation of the escarpment at both breeding colonies (Scott and Kirkpatrick, 2008). The four and a half-year lag between high rabbit density on the island and low breeding propensity for the two albatross species reflects the delayed vegetation suppression at these southern colonies. For light-mantled albatrosses, which are widely distributed on the island, the half-year lag in the response of breeding propensity is more likely to be a direct effect of the high, island-wide rabbit density.

The influence of extreme weather events and a changing climate

Understanding the effects of invasive species together with that of a changing climate are crucial to mitigating impacts on native species (Pyke et al., 2008). Subantarctic latitudes have recently experienced changes in predominant weather patterns as a result of global climate change (Thost and Allison, 2006, Le Roux and McGeoch, 2008, Lebouvier et al., 2011). For Macquarie Island, a prolonged positive phase of the Southern Annular Mode has resulted in increases in the frequency and magnitude of heavy rainfall events and increases in average daily wind speeds (Adams, 2009, Bergstrom et al., 2015). Extreme rainfall events in January, *i.e.* during the early stages of albatross chick growth, can result in high mortality, as I have shown by the lower breeding success for black-browed albatrosses. Chicks are more vulnerable at young ages because waterproof feathers have not yet developed and they have less ability to thermoregulate (Visser, 1998). Consequently, protection from extreme events

by vegetation, which provides a more stable microclimate, is likely to enhance chick survival. The interaction of high rabbit grazing pressure in an already perturbed system appears an important driver of the low breeding success observed between 2008 and 2010. For black-browed albatrosses the effect of extreme weather may have had a greater influence on breeding success than in other species, because of the lower variation in nest aspect (predominantly south-easterly), low elevation and sparse vegetation in the colony. Breeding birds and their chicks were therefore more exposed to extreme storm events driven by circumpolar deep low-pressure systems, and at greater risk of nest-site waterlogging by escarpment runoff.

The combination of an anomalously high number of extreme rainfall events and high rabbit grazing also presents the possibility of secondary effects on albatross reproductive output, with greater soil instability increasing the frequency of landslips (Ryan, 1993, Scott and Kirkpatrick, 2008). Additionally, increasing wind speeds may accelerate drying of soils between heavy rainfall events, leading to further slope erosion and potentially influence land slipping. However, the stochastic nature and spatial distribution of these events confound efforts to link them statistically to demographic trends.

Study limitations

In this study, the likelihood of incorrectly assigning a breeder as a nonbreeder, or assigning a breeder as not detected is marginally increased during the periods of poor slope condition as the number of accessible nests decreases. To negate the effects of incorrect state assignment detection probability was incorporated in the modelling. Furthermore, the results of the modelling generally show a more significant relationship between rabbit density and albatross breeding propensity compared to breeding success. This may in part be explained by the inherent natural variability of each demographic parameter. Breeding propensity is generally less variable than breeding success, and in this case only shows a response to rabbit density over the period that corresponds with the greatest rabbit damage. Therefore the differences in findings may reflect our capacity to detect a relationship for each demographic parameter.

Current status and future directions

The effects of non-predatory invasive species on the demography of native species are complex and difficult to quantify. Current research on demographic responses of seabirds to

invasive species primarily addresses predation, particularly by cats, rats or mice (Keitt et al., 2002, Cuthbert et al., 2013). Furthermore, research on the underlying processes that determine breeding propensity of seabirds largely focuses on factors such as breeding experience, adult quality and at-sea conditions (Chapter 4, Barbraud and Weimerskirch, 2005, Lee et al., 2007), with little work on the effects of nesting habitat change.

Prolonged low breeding propensity and success, as found on Macquarie Island, is likely to have ramifications for juvenile recruitment in the future, leading to a temporary decrease in the breeding population and a skewed population age structure. Due to a delayed onset of maturity and high recruitment age of albatrosses, the greatest population-level impacts on Macquarie Island may not be observed for 8-14 years after the vegetation recovers.

The success of the Macquarie Island Pest Eradication Project in removing rabbits from the island has resulted in rapid vegetation recovery (Shaw et al., 2011, Springer, 2016). There are early signs of increases in albatross breeding propensity and breeding success, and the continued recovery of slope vegetation should provide greater protection and stability in nest microclimate. However, for black-browed albatrosses, where a large proportion of the population (mean: 36.7 ± 1.2%) nest in an area where the dominant tussock species, *P. cookii* exhibits slower growth compared to the widespread *P. foliosa,* recovery of vegetation may take longer. Alternatively, cessation of heavy grazing provides an opportunity for the secondary succession of species with more vigorous recruitment, such as *P. foliosa* or *S. polaris*.

Here I show that breeding site conditions are linked to breeding propensity and success. This is important in a conservation context as for wide-ranging species, like albatrosses, apparently indirect onshore management interventions such as removing invasive species, can have a positive effect on vital rates. Affecting change in their at-sea habitats is much more challenging and achieving a conservation outcome correspondingly more difficult and complex (Wilcox and Donlan, 2007). Positive changes in vital rates, as I show, can translate into real outcomes at the population level, such that when invasive species are removed, populations can increase given more individuals are recruited into the potential breeding population by increases in chick fledging rates. By quantifying the indirect and complex effects that invasive species have on the demographics of a community of native seabird species and their subsequent population structure, I obtain greater insight into vulnerability or

resilience of each species to changes in ecosystem state and ultimately reduce the likelihood of negative and unintended consequences of future applied conservation management.

Conclusion

I found that high rabbit density was linked to low breeding propensity of subantarctic albatrosses through severe habitat degradation. For one species (black-browed albatrosses), the synergistic impacts of extreme weather events and high rabbit density explained decreases in breeding success. The future for the albatross populations following the rabbit eradication on Macquarie Island looks positive, given that reproductive ability has already improved. Our findings illustrate the importance of breeding site characteristics on vital rates in albatrosses and show that integrating terrestrial threatening processes is important when assessing population viability and the development of management policy for predominantly marine species.

Acknowledgements

The authors would like to thank Rosemary Gales for her commitment to albatross monitoring on Macquarie Island over the last two decades, Rowan Trebilco for the contribution of photos used in this manuscript, Jenny Scott and Keith Springer for insights into historical Macquarie Island vegetation changes, and Guillaume Souchay for technical assistance. The Australian Antarctic Division through the Australian Antarctic Science Program (Project numbers: 751, 2569, 4112) has supported this research at Macquarie Island.

Supporting Information

Table S1 Input GEMACO sentences for the time-dependent model analysis in E-Surge. t refers to time and f refers to previous breeding state, 1 to 63 refers to time periods 1952 to 2015 + others accounts for the parameters not accounted for in the main sentence, i stands for constant (refer to E-Surge manual). Seasons 1994/95 to 2014/15 correspond time steps 43 to 63 and are the subject of the analysis.

		Black-browed albatross	Grey-headed albatross	Light-mantled albatross
Initial state (*i*)		i	i	i
Transition (ψ)	Survival (ϕ)	t(1:42) + t(43_63)	t(1:42) + t(43_63)	t(1:42) + t(43_63)
	Return (r)	t(1:42) + t(43_63)	[t(43_63) + f(1,2 3 4 5 6)] + others	[t(43_63) + f(1,2 3 4 5 6)] + others
	Breeding (β)	t(1:42) + t(43_63)	[t(43_63) + f(1,3 5 7 8 9)] + others	[t(43_63) + f(1,3 5 7 8 9)] + others
	Breeding success (γ)	t(1:42) + t(43_63)	t(1:42) + t(43_63)	t(1:42) + t(43_63)
Event (Ω)	Detection (P)	firste + nexte.[t(43_63) + f(1 2,3)] + others	firste + nexte.[t(1:42) + f(1 2,3).[i + t(43_62) * rabbit $_{lag2.5}$]]	firste + nexte.[f.[t(1:42) + [i + t(43_62) * rabbit $_{lag1.5}$]]]
	Breeding outcome uncertainty (k)	i	i	i

Table S2 Multi-event capture-recapture modelling of black-browed, grey-headed and light-mantled albatrosses at Macquarie Island, testing the influence of island-wide rabbit density on breeding propensity, and rabbit density, extreme January rainfall events (80th percentile) on breeding success in 1994-2015.

		Model	N_p	Deviance	p ANODEV	R^2 (%)	Slope (±SE)
Breeding propensity (β)	*Black-browed albatross*						
		cst	1	5958.20			
		t	20	5868.71			
		t + lin	2	5893.55	**<0.001**	72.2	-0.89±0.23
		t + rabbit$_{lag4.5}$	2	5890.56	**<0.001**	75.6	-0.80±0.15
		t + lin + rabbit$_{lag4.5}$	3	5885.24	**0.009**	33.4	-0.31±0.15
	Grey-headed albatross						
		cst	1	10142.67			
		t	20	10026.52			
		t + lin	2	10107.72	**0.012**	30.1	-1.01±0.32
		t + rabbit $_{lag4.5}$	2	10106.43	**0.010**	31.2	-0.83±0.20
		t + lin + rabbit $_{lag4.5}$	3	10099.95	0.198	9.6	-0.32±0.21
	Light-mantled albatross						
		cst	1	29115.48			
		t	20	29069.85			
		t + lin	2	29114.79	0.606	1.5	-0.51±1.40
		t + rabbit $_{lag05}$	2	29106.33	**0.048**	20.1	-2.13±0.40
		t + lin + rabbit$_{lag05}$	3	29100.17	**0.012**	31.7	-1.30±0.70
Breeding success (γ)	*Black-browed albatross*						
		cst	1	5956.90			
		t	20	5868.71			
		t + lin	2	5952.86	0.365	4.6	-0.13±0.10
		t + rabbit $_{lag35}$	2	5934.24	**0.023**	25.7	-0.33±0.11
		t + lin + rabbit$_{lag35}$	3	5927.59	**0.015**	30.0	-0.35±0.11
		t + rain	2	5932.04	**0.016**	28.2	-0.32±0.10
		t + lin + rain	3	5928.36	**0.017**	29.1	-0.32±0.10
		t + rabbit $_{lag35}$ + rain	3	5927.45	**0.014**	30.2	
		t + lin + rabbit $_{lag35}$ + rain	4	5911.14	**<0.001**	49.6	
	Grey-headed albatross						
		cst	1	10088.23			
		t	20	10000.70			
		t + lin	2	10087.00	0.619	1.4	-0.07±0.12
		t + rabbit$_{lag35}$	2	10085.15	0.428	3.5	-0.13±0.13
		t + lin + rabbit$_{lag35}$	3	10084.90	0.796	0.4	-0.10±0.13
		t + rain	2	10086.95	0.611	1.5	-0.06±0.11
		t +lin + rain	3	10084.92	0.804	0.4	-0.03±0.11
	Light-mantled albatross						
		cst	1	29210.58			
		t	20	29068.52			
		t + lin	2	29203.02	0.328	5.3	0.13±0.08
		t + rabbit$_{lag0}$	2	29191.02	0.107	13.8	0.18±0.07
		t + lin + rabbit$_{lag0}$	3	29183.23	0.105	14.7	0.20±0.08
		t + rain	2	29210.15	0.819	0.3	0.02±0.08
		t + lin + rain	3	29200.26	0.559	2.1	-0.05±0.08

* Terms are N_p, the number of structural parameters, ANODEV, analysis of deviance (Grosbois et al., 2008), R^2, the proportion of variance explained by the test covariate. The three standardised environmental covariates used are *rabbit*, mean monthly modelled island-wide rabbit density (Terauds et al., 2014), *rain,* number of January days of high rainfall (80th percentile of 1995-2014 data) and *wind,* number of January days with high wind events (80th percentile of 1995-2014 data). Models *cst*, *t*, *lin,* correspond to constant, time-dependent and linear trend models tested on reproductive rates of breeding propensity (β) and breeding success (γ).

Table S3. Summary table of encountered black-browed albatrosses on Macquarie Island according to state from 1994/95 to 2014/15.

		Successful breeders	Failed breeders	Breeders with unknown breeding outcome	Nonbreeders	Total
Black-browed albatross	1994/95	42	25	2	25	94
	1995/96	45	26	0	21	92
	1996/97	46	28	1	26	101
	1997/98	36	49	0	37	122
	1998/99	39	51	0	22	112
	1999/00	39	44	0	24	107
	2000/01	30	43	8	10	91
	2001/02	38	33	2	31	104
	2002/03	45	31	0	38	114
	2003/04	38	38	1	10	87
	2004/05	56	15	3	35	109
	2006/07	31	45	0	18	94
	2007/08	21	18	2	5	46
	2008/09	27	14	0	15	56
	2009/10	16	33	2	8	59
	2010/11	8	35	0	31	74
	2011/12	10	28	0	43	81
	2012/13	8	9	0	5	22
	2013/14	13	22	0	35	70
	2014/15	22	18	0	35	75

Table S4. Summary table of encountered grey-headed albatrosses on Macquarie Island according to state from 1994/95 to 2014/15.

		Successful breeders	Failed breeders	Breeders with unknown breeding outcome	Nonbreeders	Total
Grey-headed albatross	1994/95	78	26	9	69	182
	1995/96	99	46	0	72	217
	1996/97	106	41	0	36	183
	1997/98	82	51	0	54	187
	1998/99	72	76	0	33	181
	1999/00	59	42	2	45	148
	2000/01	84	52	1	15	152
	2001/02	81	40	1	34	156
	2002/03	66	56	0	45	167
	2003/04	118	46	3	46	213
	2004/05	65	23	0	40	128
	2006/07	45	85	0	29	159
	2007/08	58	19	0	9	86
	2008/09	25	12	3	12	52
	2009/10	25	21	2	7	55
	2010/11	11	22	0	28	61
	2011/12	24	18	0	21	63
	2012/13	12	12	0	3	27
	2013/14	23	19	0	13	55
	2014/15	60	22	0	26	108

Table S5. Summary table of encountered light-mantled albatrosses on Macquarie Island according to state from 1994/95 to 2014/15.

Light-mantled albatross

	Successful breeders	Failed breeders	Breeders with unknown breeding outcome	Nonbreeders	Total
1994/95	161	129	12	6	308
1995/96	141	132	17	1	291
1996/97	148	193	7	5	353
1997/98	173	124	4	38	339
1998/99	162	125	2	37	326
1999/00	105	116	3	0	224
2000/01	161	147	2	27	337
2001/02	98	150	2	26	276
2002/03	224	130	3	51	408
2003/04	139	84	1	24	248
2004/05	156	44	0	26	226
2006/07	62	67	1	14	144
2007/08	79	67	0	14	160
2008/09	86	31	0	28	145
2009/10	111	51	1	32	195
2010/11	49	69	3	30	151
2011/12	114	90	1	39	244
2012/13	40	76	1	25	142
2013/14	84	78	0	17	179
2014/15	77	57	0	17	151

Figure S1 Time series (1995-2014) of rabbit driven degradation at the black-browed and grey-headed breeding colony the south-west slopes of Macquarie Island. The images taken from March 2007 show a large scar from a landslide triggered by heavy vegetation suppression caused by rabbit grazing. Images sourced from J. Scott.

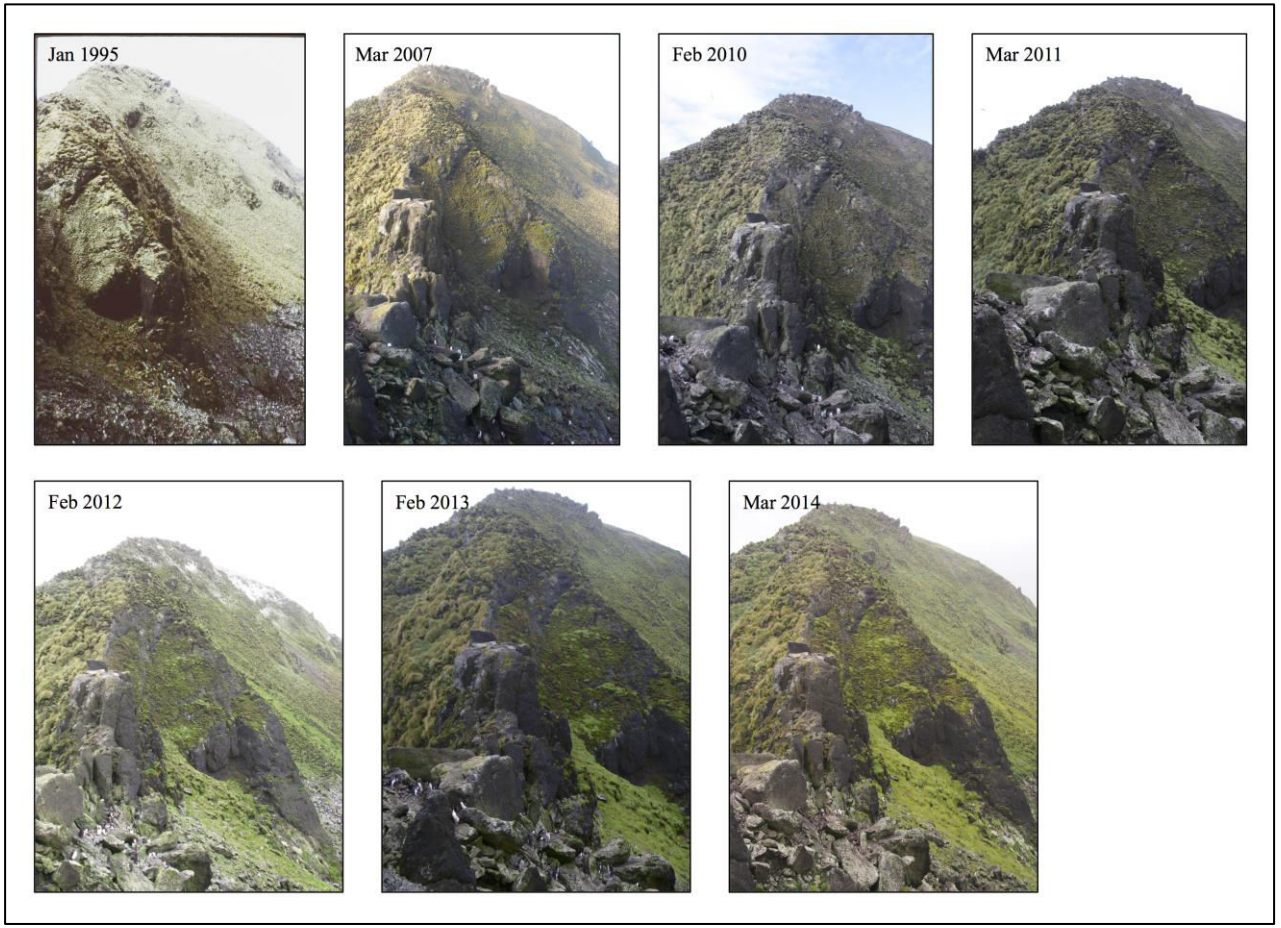


Figure S2 Time series (1995-2014) of rabbit driven degradation at the black-browed and grey-headed breeding colony the south-west slopes of Macquarie Island. The bottom right quadrant of each image represents the main breeding area of black-browed albatross. The first image taken in January 1995 shows tussock *Poa foliosa* as the dominant vegetation in this area, by March 2007 heavy rabbit grazing saw a transition to dead tussock and mud which is followed by the slow colonization of this area by *Leptinella plumosa* (2010-2014). Images sourced from J. Scott.

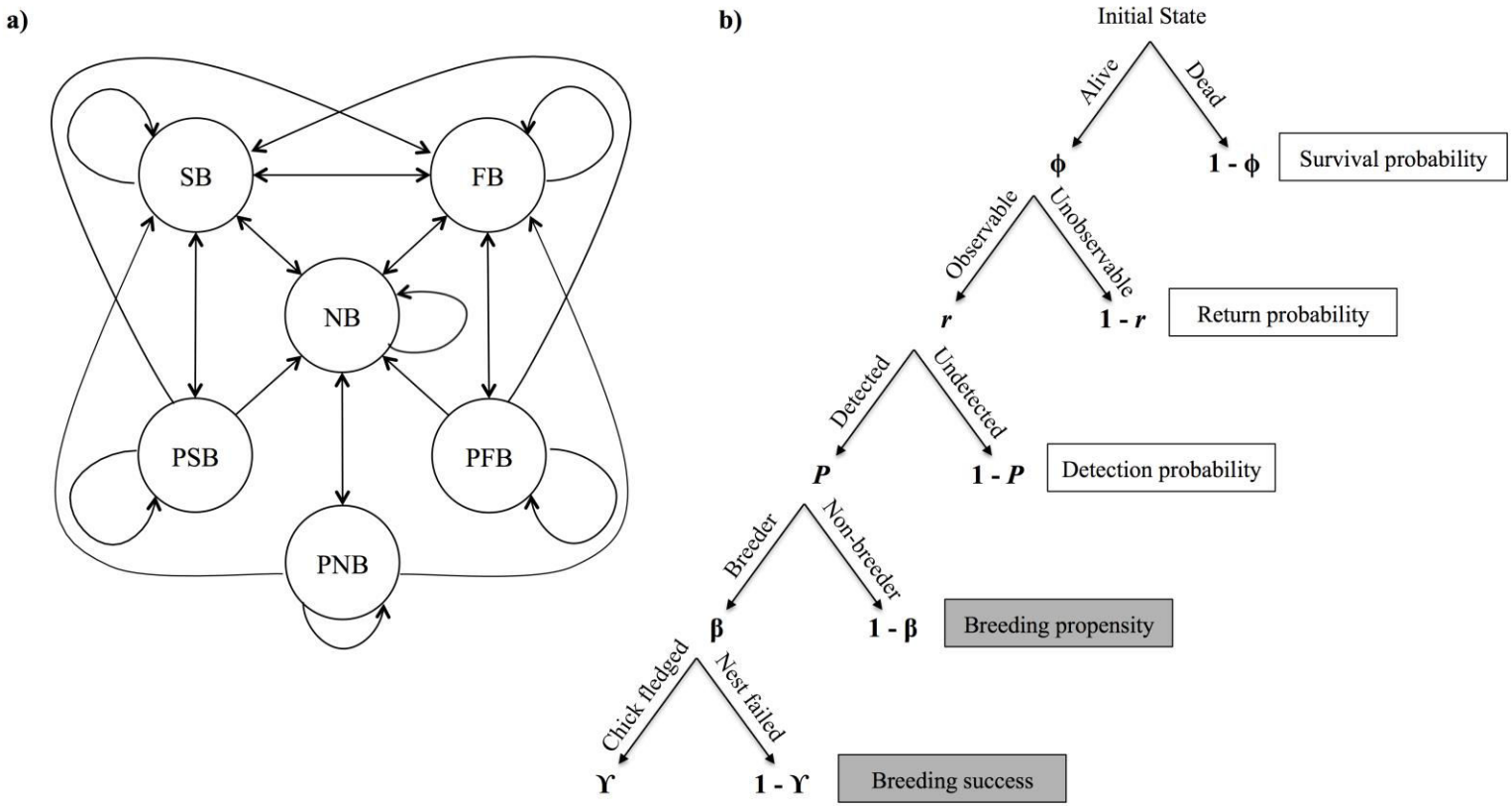


Figure S3 a) Possible state transition pathways of adult albatrosses at Macquarie Island (black-browed, grey-headed and light-mantled albatrosses) including observable states; successful breeder (SB), failed breeder (FB), nonbreeder (NB); and unobservable states, post-successful breeder (PNB), post-failed breeder (PFB) and post nonbreeder (PNB). b) Probability estimation of demographic parameters of individual survival (ϕ), return (r), detection (P), breeding (β) and success (γ) associated with progressing from the initial state (encountered as SB or FB) to fledging a chick.

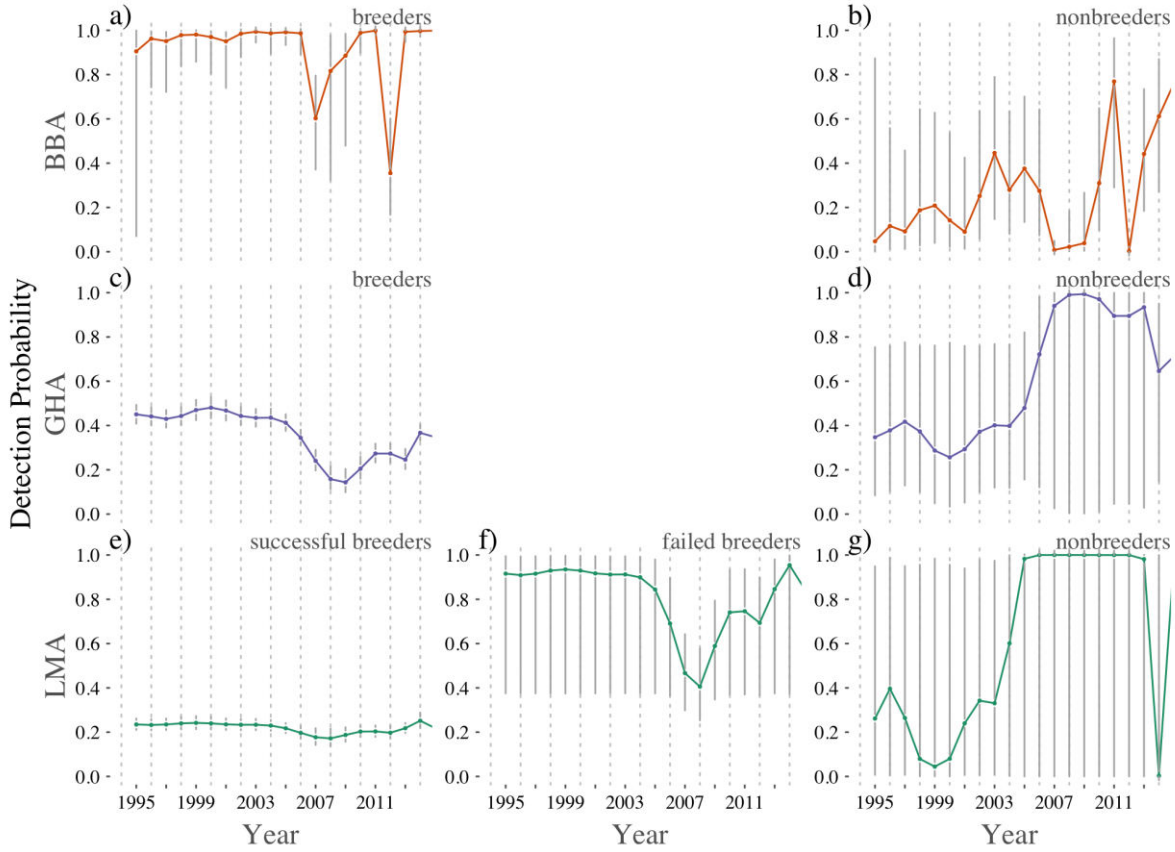


Figure S4 Annual variation in detection probability of experienced adult breeders at Macquarie Island (black-browed, BBA, orange; grey-headed, GHA, purple; and light-mantled albatrosses, LMA, green), modelled as time-dependent (solid coloured lines) and grouped by breeding status (including failed breeders for light-mantled albatrosses).

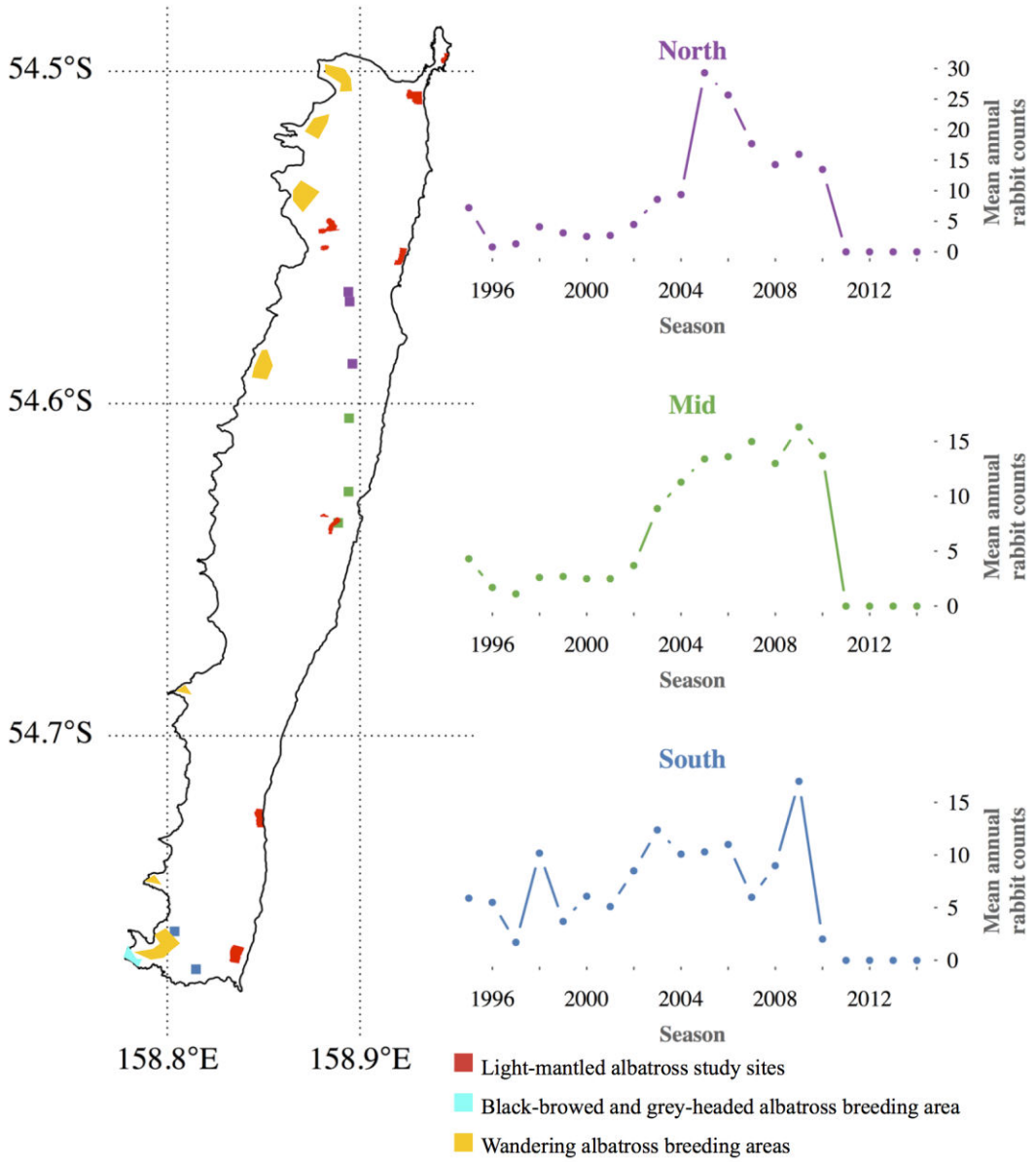


Figure S5 Spatiotemporal patterns in rabbit density from north (purple squares), mid (green squares) and south (blue squares) rabbit count areas (annual mean of monthly rabbit counts from 1 ha plots) in relation to albatross breeding areas on subantarctic Macquarie Island (Terauds et al. 2014).

Appendix S1 Input GEPAT matrices for analysis in E-Surge.

Initial State (i)

$$i = [i \quad 1-i \quad - \quad - \quad - \quad -]$$

Survival (ϕ) transition:

$$\phi_t\psi = \begin{bmatrix} \phi & - & - & - & - & - & 1-\phi \\ - & \phi & - & - & - & - & 1-\phi \\ - & - & \phi & - & - & - & 1-\phi \\ - & - & - & \phi & - & - & 1-\phi \\ - & - & - & - & \phi & - & 1-\phi \\ - & - & - & - & - & \phi & 1-\phi \\ - & - & - & - & - & - & \dagger \end{bmatrix}$$

Return (r) transition:

$$r_t\psi = \begin{bmatrix} r & 1-r & - & - & - & - & - & - & - & - \\ - & - & r & 1-r & - & - & - & - & - & - \\ - & - & - & - & r & 1-r & - & - & - & - \\ - & 1-r & - & - & - & - & r & - & - & - \\ - & - & - & 1-r & - & - & - & r & - & - \\ - & - & - & - & - & 1-r & - & - & r & - \\ - & - & - & - & - & - & - & - & - & \dagger \end{bmatrix}$$

Breeding (β) transition:

$$\beta_t\psi = \begin{bmatrix} \beta & 1-\beta & - & - & - & - & - & - & - & - & - & - & - \\ - & - & 1 & - & - & - & - & - & - & - & - & - & - \\ - & - & - & \beta & 1-\beta & - & - & - & - & - & - & - & - \\ - & - & - & - & - & 1 & - & - & - & - & - & - & - \\ - & - & - & - & - & - & \beta & 1-\beta & - & - & - & - & - \\ - & - & - & - & - & - & - & - & 1 & - & - & - & - \\ - & - & 1-\beta & - & - & - & - & - & - & \beta & - & - & - \\ - & - & - & - & - & 1-\beta & - & - & - & - & \beta & - & - \\ - & - & - & - & - & - & - & - & 1-\beta & - & - & \beta & - \\ - & - & - & - & - & - & - & - & - & - & - & - & \dagger \end{bmatrix}$$

Breeding success (γ) transition:

$$\gamma_t\psi = \begin{bmatrix} \gamma & 1-\gamma & - & - & - & - & - \\ - & - & 1 & - & - & - & - \\ - & - & - & 1 & - & - & - \\ \gamma & 1-\gamma & - & - & - & - & - \\ - & - & 1 & - & - & - & - \\ - & - & - & - & 1 & - & - \\ \gamma & 1-\gamma & - & - & - & - & - \\ - & - & 1 & - & - & - & - \\ - & - & - & - & - & 1 & - \\ \gamma & 1-\gamma & - & - & - & - & - \\ \gamma & 1-\gamma & - & - & - & - & - \\ \gamma & 1-\gamma & - & - & - & - & - \\ - & - & - & - & - & - & \dagger \end{bmatrix}$$

Detection (P) event:

$$P_t\Omega = \begin{bmatrix} 1-P & P & - & - \\ 1-P & - & P & - \\ 1-P & - & - & P \\ 1 & - & - & - \\ 1 & - & - & - \\ 1 & - & - & - \end{bmatrix}$$

Breeding outcome uncertainty (k) event:

$$k_t\Omega = \begin{bmatrix} 1 & - & - & - & - \\ - & 1-k & - & - & k \\ - & - & 1-k & - & k \\ - & - & - & 1 & - \end{bmatrix}$$

Chapter 4

Deconstructing the influence of three major types of threat on the demography of an albatross community

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Abstract

Climate change, fisheries and invasive species represent three of the most pervasive conservation threats to seabirds globally. Understanding the relative influence and compounding nature of marine and onshore threats on the demographic rates of seabird communities is vital for evidence-based conservation planning. Using 20 years of capture-mark-recapture data from four sympatric species of albatrosses (black-browed *Thalassarche melanophris*, grey-headed *T. chrystostoma*, light-mantled *Phoebetria palpebrata* and wandering albatrosses *Diomedea exulans*), I quantified the temporal variability in survival, breeding propensity and success. In three species (excluding the wandering albatrosses), we assessed the influence of fisheries, oceanic and onshore change were assessed to give insight into future population viability. Two oceanic variables had a major influence on survival and breeding success in black-browed, grey-headed and light-mantled albatrosses. The Southern Annular Mode (SAM) explained between 22.9-40.9% and 22.2-33.4% of the temporal variability in survival and breeding success, respectively. Relationships were positive in all cases except between SAM the breeding success of light-mantled albatrosses. Similarly, the El Niño Southern Oscillation (ENSO) Index explained 24.9-43.1% of the variability in survival, with higher survival rates during La Niña events. Habitat degradation caused by high density of rabbits *Oryctolagus cuniculus* explained 20.0-75.6% of the temporal variability in breeding propensity, which declined in all three species. For black-browed albatrosses, effort in New Zealand trawl and south-west Atlantic longline fisheries effort had, respectively, positive and negative relationships with survival, and explained 21.2% and 22.3%-31.6% of the variability, respectively. These findings suggest that managing drivers of negative demographic trends that may be more easily controlled, such as fisheries and habitat degradation, will be a viable option for some species (*e.g.* black-browed albatross) but less effective for others (*e.g.* light-mantled albatross), as opposed to drivers which are not easily mitigated, such as climate change. Furthermore, my results illustrate the need to integrate fisheries, oceanic and onshore threatening processes when assessing demographic variability and formulating the appropriate management response.

Introduction

Climate-driven changes in the marine ecosystem affect wild animal populations in complex ways (Constable et al., 2014), and understanding how populations respond to environmental change across their distribution is vital for predicting their viability (Vargas et al., 2007, Lehodey et al., 2006). In the Southern Ocean, climate change is driving regional trends in sea

ice extent and seasonality (Stammerjohn et al., 2012), causing major oceanic fronts to move southward (Sokolov and Rintoul, 2009) increasing wind intensity, particularly the southerly component (Turner et al., 2009) and enhancing eddy activity (Meredith and Hogg, 2006). Furthermore, large-scale climate cycles that are coupled with Southern Ocean processes over decadal scales, such as the Southern Annular Mode (SAM) and the El Niño Southern Oscillation (SOI) are also influenced by climate change, with major demographic consequences predicted for multiple populations (Murphy et al., 2007, Forcada and Trathan, 2009).

For marine predator populations, climate-driven changes in physical oceanographic and atmospheric conditions have the potential to influence individual foraging efficiency by affecting the accessibility and predictability of prey (Lea et al., 2006), or the energetic cost of reaching foraging areas (Weimerskirch et al., 2012). However, climate-driven changes are not occurring in isolation, but simultaneously with evolving fisheries that overlap with the foraging habitat of numerous seabird species (Tuck et al., 2003). Through mechanisms such as incidental mortality (bycatch) (Goldsworthy and Page, 2007, Anderson et al., 2011), discarding of non-target catch and offal (Bartumeus et al., 2010, Patrick et al., 2015) and increased competition for resources (Cury et al., 2011), fisheries can influence survival or induce changes in foraging behaviour that affects breeding frequency or success. For small populations, simultaneous negative effects on both survival and reproductive output can be catastrophic, driving rapid declines and leading to local population extinctions (Weller et al., 2014, Chilvers and Meyer, 2017).

Information about the processes that influence demographic variability is fundamental to evidence-based conservation planning. However, albatrosses are highly philopatric, long-ranging pelagic foragers, and their broad foraging ranges make it difficult to quantify these processes. Albatrosses have a long-delayed onset of maturity, albatrosses exhibit low survival prior to recruitment (typically > 10 years), after which breeding occurs either annually or biennially, depending on species (Warham, 1990, Jouventin and Dobson, 2002). Adult survival is naturally high, with individuals of some species living up to 50 years (Weimerskirch et al., 1987). Their slow life cycle combined with high survival rates means that any additional increase in mortality or decrease in reproductive output has considerable consequences for population viability, even if these might take some time to become visible in the population (Phillips et al., 2016). Historical decreases in adult survival due to

incidental bycatch by longline and trawl fisheries have been identified as the greatest contributor to observed rapid and widespread population declines of multiple albatross species (Gales and Robertson, 1998, Dunn et al., 2007, Phillips et al., 2016). Over the last decade, wider implementation of technological solutions that mitigate bycatch, such as the use of exclusion devices (Maree et al., 2014), integrated-weight lines (Robertson et al., 2010) or underwater line-setters (Gilman et al., 2003) have slowed or stopped declines or resulted in minor increases in a small number of colonies (Inchausti and Weimerskirch, 2001, Robertson et al., 2014). However, as their distributions often span multiple regional, national and international fisheries management boundaries and there is wide variation in the implementation of mitigation measures and many gaps remain in our knowledge of the key drivers of population change for most albatross populations (Cooper et al., 2006, Phillips et al., 2016).

Breeding on land, albatrosses can face pressures at the colony that affect reproduction and survival, including habitat degradation and the impacts of invasive species. Introduced mammals are particularly problematic for seabirds and can transform island ecosystem dynamics through predation (Cuthbert and Hilton, 2004), competition for habitat (Brothers and Bone, 2008) or habitat degradation (Chapter 3). As islands often represent the only breeding habitat for many seabird species, changes in habitat quality or the influence of invasive species can have a profound effect on entire communities.

With different pressures on life history traits, each species within a community will respond differently to environmental variation, be it marine (climate, fisheries) or onshore (terrestrial and local weather). Consequently, integrated studies addressing the effects of both at-sea (e.g. oceanographic, atmospheric, climatic or fisheries) and onshore factors (e.g. habitat, weather or invasive species) on the demographic rates of multiple species are needed to provide a synthetic understanding of albatross demography. Quantification of oceanic and onshore influences provides the evidence base to support conservation action reducing outcome uncertainty. Specifically, it allows the identification of drivers that are more easily managed (e.g. invasive species, fisheries), and which can buffer against those that are not (e.g. climate change).

Four species of Southern Ocean albatrosses breed on Macquarie Island; black-browed *Thalassarche melanophris*, grey-headed *Thalassarche chrysostoma*, light-mantled

Phoebetria palpebrata, and wandering albatrosses *Diomedea exulans*. With the exception of light-mantled albatrosses, these populations are small (<80 breeding pairs), and therefore at risk of local extinction; for this reason, the community is a high biogeographic priority for conservation. At Macquarie Island, declines in survival of wandering albatross have been linked to bycatch in tuna longline fisheries (de la Mare and Kerry, 1994, Terauds et al., 2006b), although no such links have been established for black-browed or grey-headed albatrosses (Terauds et al., 2005). More recently, declines in the breeding propensity of black-browed, grey-headed and light-mantled albatrosses have been attributed to wide scale habitat degradation caused by high rabbit *Oryctolagus cuniculus* populations; for black-browed albatrosses, the combination of heavy rainfall events and high rabbit density also cause substantial reductions in breeding success (Chapter 3).

To understand the influence of fisheries, oceanic and onshore factors on demography of the Macquarie Island albatross community, I aimed to 1)) determine annual changes in survival, breeding probability and breeding success of each species; 2) compare and contrast demographic variability across species, and; 3) assess the roles of various environmental processes on demography

Methods

Field methods

Three of the four albatross species breeding at subantarctic Macquarie Island (54.6° S, 158.9° E) occur in small numbers; approximately 40, 80 and five breeding pairs of black-browed, grey-headed and wandering albatrosses, respectively. In contrast, there are approximately 2 150 breeding pairs of light-mantled albatrosses (DPIPWE, 2014). All accessible albatross chicks of each species were banded with stainless steel leg bands between 1995 and 2014 (seasons 1994/95 and 2013/14), except for light-mantled albatross chicks, where this applied only to chicks within seven study areas (~10% of total island breeding population). From 1994-2003, any unbanded adults that could be captured safely were also banded. Visits to nests with eggs in early incubation allowed breeding adults to be identified, and nests were also visited towards the end of chick-rearing to band chicks, providing data on survival to fledging. Any banded nonbreeding adults observed in the colony were also recorded.

Demographic analysis

Demographic parameters were modelled using 20 years (1995-2014) of capture-mark-recapture data. Demographic parameters - survival (Φ), return (r), breeding propensity (β), breeding success (γ), and detection probability (p) - were estimated using a hidden Markov model framework, in which it was assumed that individuals transition between different states (e.g. breeder, nonbreeder, etc.; see Chapter 3, Fig. S3a) over time, with transitions between states described by a Markov chain. The state of an individual was assumed not to be directly observable, but rather observed indirectly by means of an event (hereafter referred to as an encounter). Encounters were assumed to be dependent on the true, but unobserved, state of the individual. Encounter histories for each individual were used to fit a population-level model, with model parameters dependent on environmental parameters as described below. Models were fitted in the E-Surge 1.9.0 software (Choquet et al., 2009b) using maximum likelihood estimation.

Individual encounter histories (total birds: black-browed, n = 225; grey-headed, n = 513; light-mantled, n = 1215; and wandering albatrosses, n = 78) consisted of four observable adult states (successful breeder, failed breeder, nonbreeder and breeder with uncertain breeding outcome) and three unobservable states (post-successful breeder, post-failed breeder, post nonbreeder) (Chapter 3, Fig. S3a; Chapter 3, Table 3-5; & Table S1). The unobservable post-breeding states were included to account for differences in year-to-year transitional breeding propensity (ψ) generated by biennial breeding behaviour (Barbraud and Weimerskirch, 2012). A small proportion of breeding outcomes were also unknown, due to failure to revisit the nests late in the breeding season (1.5%, 1.1%, 1.3% and 2.3% of observations for black-browed, grey-headed, light-mantled and wandering albatrosses). State uncertainty was incorporated in an event matrix, allowing the likelihood of being a successful breeder to be assessed (Pradel, 2005, Gimenez et al., 2012).

To remain tractable but functional due to the small population sizes, the analysis was restricted to adult demographic parameters by suppressing all chick, juvenile and nonbreeding states before the first breeding attempt. It was also assumed that the demographic parameters were not affected by age, experience, sex or quality. Further, I expected similar survival, regardless of state for each species. For grey-headed, light-mantled and wandering albatrosses (biennial breeders) the probability of return and breeding for successful breeders was estimated separately to failed and nonbreeders for the time-dependent models. In contrast, black-browed albatross (annual breeders) estimates were

derived using a time-dependent (*t*) model for all demographic parameters. For all species, time-dependent parameters were retained when modelling the demographic parameter of interest.

Nest accessibility for grey-headed and light-mantled albatrosses was affected by severe habitat degradation due to heavy rabbit grazing during the 2000s, affecting estimates of the detection probability (*p*), and so rabbit density was included as a covariate in the modelling of detection probability for these species (Table S2 & Fig. S1). The majority of black-browed albatrosses nest in a clustered group lower down on the escarpment, making them more accessible. Detection probabilities were also estimated separately for breeders and nonbreeders because bands are easier to read on a nesting adult (Fig. S1). Complete model input notation, probability estimation and transition matrix structures are contained in Table S2; Chapter 3, Fig. S3b; and Chapter 3, Appendix S1.

To test for goodness-of-fit, encounter histories were transformed to single-state and assessed using U-Care 2.3.2 software, including tests for transience (Pradel et al., 2005, Choquet et al., 2009a). Tests for trap-dependence (Test 2: 2.CT + 2.Cl) were excluded since the model structure accounted for differences in breeding propensity based on previous breeding states, characteristic of skip-breeding (Barbraud and Weimerskirch, 2012). Correction for lack of fit within the populations was applied using an over-dispersion factor (ĉ) (Lebreton et al., 1992).

A sequence of models was fitted for each species to disentangle the various influences on demography. First, single-predictor models were fitted, using each predictor variable in turn. Significant covariates were then grouped into fisheries, oceanic and onshore models to provide a synthetic overview of how the vital rates were affected by each major threat type. Finally, all significant covariates were integrated into a global model to determine the total demographic variability that could be explained by the covariates and highlight uncertainty when explaining temporal variability.

The significance of environmental covariates on each demographic parameter modelled was evaluated using analysis of deviance tests, and the strength of the effect ascertained by the total variation explained by the covariates (Grosbois et al., 2008). Wandering albatrosses were excluded from the environmental analysis due to their small population size. Basic models described the total variation explained by the covariates (R^2). In addition, because

long-term temporal trends in the environmental covariate and demographic rate can obscure the relationship between them, de-trended models that provide a measure of short-term variation were implemented. The de-trended models described the total variation explained by the covariates when temporal trends were removed from the variable and the demographic rate (de-trended R^2). The basic and de-trended models are regarded as explaining long-term and short-term variability, respectively. Model selection was based on Akaike's information criterion (AIC), whereby the model with the lowest AIC (where $\Delta QAIC > 2$) was preferred (Burnham and Anderson, 2002).

Covariates

Fisheries and oceanic covariates were taken from the spatial extent of the foraging distribution of each species determined by previous tracking studies (Fig. 2) (Chapter 2). Each covariate consisted of a time series of values averaged from weekly and monthly data to give an annual mean across the foraging distribution. The temporal range of each environmental covariate was aligned to the appropriate stage of the breeding cycle for each species (Table 1).

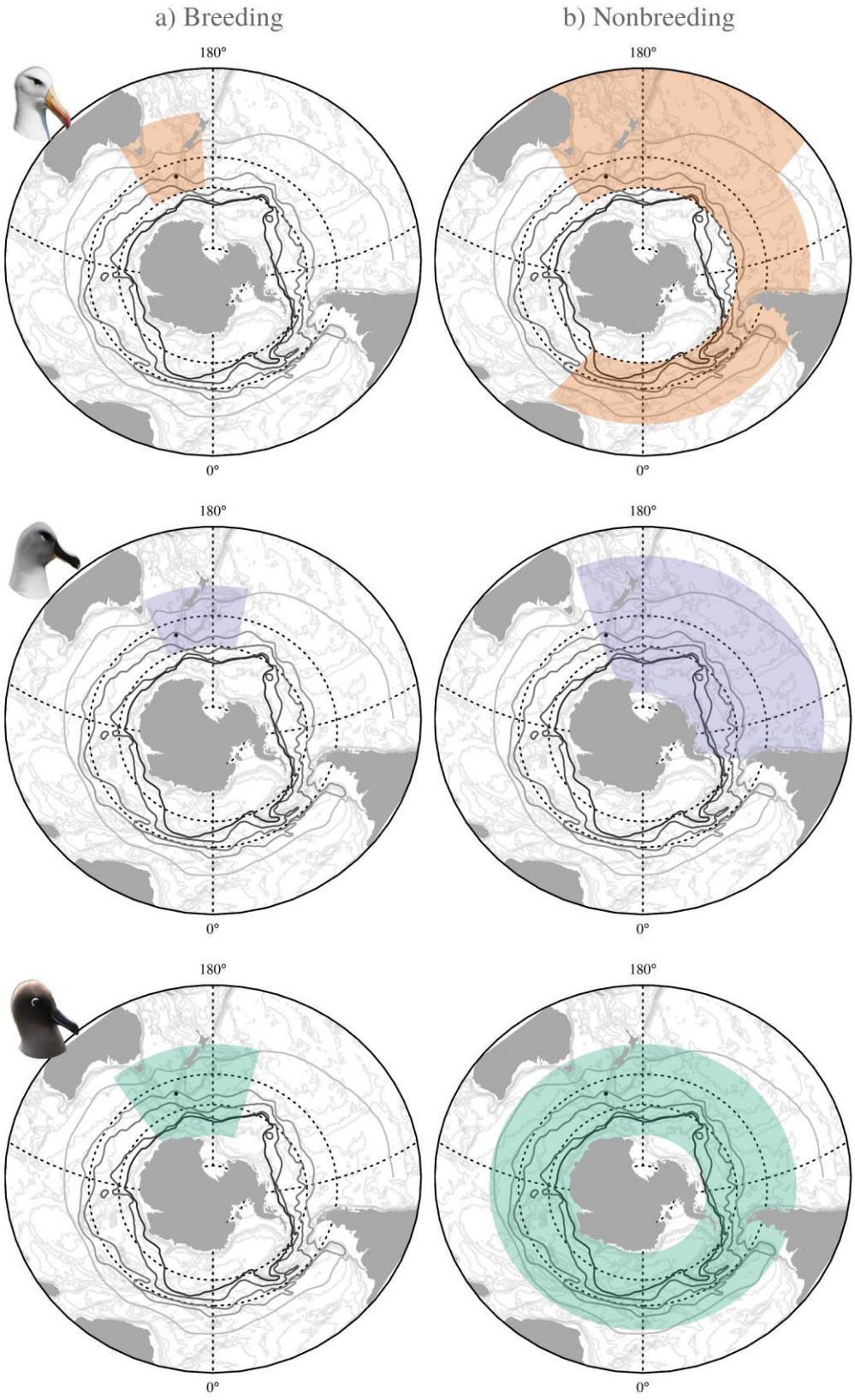

Figure 2 Spatial extent of oceanographic and atmospheric covariates incorporated in the demographic modelling of Macquarie Island black-browed (orange), grey-headed (purple) and light-mantled (green) albatrosses during breeding (a) and nonbreeding (b) periods.

Table 1 Source of fisheries, oceanic and habitat data used in the demographic models.

	Covariate	Acronym	Black-browed			Grey-headed			Light-mantled		
			ϕ	β	γ	ϕ	β	γ	ϕ	β	γ
Fisheries	Australian longline	ausLL	a			a					
	Australian trawl	ausTR	a			a					
	CCAMLR longline	ccamlrLL	a								
	CCAMLR trawl	ccamlrTR	a								
	CCSBT longline	ccsbstTR	a			a					
	Chilean longline	chileLL	a								
	Falkland Islands longline	falklandsLL	a								
	Falkland Islands trawl	falklandsTR	a								
	ICCAT longline	iccatLL	a								
	IOTC longline	iotcLL	a								
	New Zealand longline	nzLL	a			a					
	New Zealand trawl	nzTR	a			a					
	SPRFMO longline	sprfmoLL	a			a					
	WCPFC longline	wcpfcLL	a			a					
Oceanic	Southern Annular Mode Index	sam	b	b	b	b	b	b	b	b	b
	Southern Oscillation Index	soi	b	b	b	b	b	b	b	b	b
	Sea Surface Temperature (°C)	sst	c	c	c	c	c	c	c	c	c
	Sea Surface Height Anomaly (mm)	ssha	c	c	c	c	c	c	c	c	c
	Sea ice extent (sea ice concentration >= 15%)	ice	c	c	c	c	c	c	c	c	c
	Wind speed (m/s)	wind	c	c	c	c	c	c	c	c	c
	Meridional wind (u component)	wind_u	c	c	c	c	c	c	c	c	c
	Zonal wind (v component)	wind_v	c	c	c	c	c	c	c	c	c
Habitat	Rainfall (mm, number of days in 80th percentile of long-term average)	rain			d			d			d
	Rabbit density (modelled monthly total)	rabbits		e	e		e	e		f	f

Legend

summarised over the previous nonbreeding and the current breeding period and corresponding distribution from tracking data

summarised over the previous nonbreeding period and nonbreeding distribution from tracking data

summarised over the current breeding period and breeding distribution from tracking data

a	monthly total
b	monthly mean (with six month lags 0-3 years)
c	monthly mean
d	January
e	monthly total (with six month lags 3.5-4.5 years)
f	monthly total (with 0 and 6 month lags)

NOTE: Longline (number of hooks) and trawl (number of hours) fisheries effort data in 5x5 degree resolutions. Data sources: Australian Fisheries Management Authority (ausLL, ausTR), (chileLL), Commission for the Conservation of Antarctic Marine Living Resources (ccamlrLL, ccamlrTR), Commission for the Conservation of Southern Bluefin Tuna (ccsbtLL), Falkland Islands Government Fisheries Department (falklandsLL, falklandsTR), International Commission for the Conservation of Atlantic Tunas (iccatLL), Indian Ocean Tuna Commission (iotcLL), New Zealand Ministry for Primary Industries (nzLL, nzTR), South Pacific Regional Fisheries Management Organisation (sprfmoLL), Western and Central Pacific Fisheries Convention (wcpfcLL), Marshall (2003)(sam), Australian Department of Environment and Energy (soi), Australian Bureau of Meteorology (rain), National Oceanic and Atmospheric Administration Earth System Research Laboratory Physical Sciences Division (sst, wind, wind_u, wind_v), National Centre for Space Studies France (ssha), (ice), Terauds et al. (2014) (rabbits).

Oceanic covariates were derived from monthly sea ice extent (ice), sea surface temperature (sst), sea surface height anomaly (ssha), wind speed (wind), meridional wind (wind_v) and zonal wind (wind_u). Large-scale climate indices the Southern Annular Mode (SAM) and Southern Oscillation Index (SOI) were also included (Table 1). For albatrosses, these covariates may act directly by affecting the energetic costs associated with flight to foraging grounds, or indirectly by influencing prey availability or accessibility. As temporal lags are likely to exist between changes in SAM and SOI and the responses of prey populations and the vital rates of seabirds (Barbraud and Weimerskirch, 2003), lags from 0 to 3 years were tested for SAM and SOI.

Fisheries effort was included in black-browed and grey-headed albatross survival models across their breeding and nonbreeding distributions. These species commonly associate with fisheries vessels and are killed incidentally by fishing gear (Phillips et al., 2016). Thus, fisheries effort was expected primarily to act as a proxy for elevated mortality risk, although the discards provide a food resource, from which the benefit may outweigh the negative effects of bycatch (Granadeiro et al., 2014, Mariano-Jelicich et al., 2014). Fisheries covariates were not included in the models for light-mantled albatrosses because they are not regularly caught as bycatch and are thought to be competitively excluded from attending fisheries vessels (Phillips et al., 2005a). Fisheries covariates comprised monthly trawl and longline effort at 5x5 degree resolution obtained from regional fisheries management organisations in the form of the number of hooks set or the number of hours trawled (Table 1).

Onshore covariates from Chapter 3 were included in the global breeding propensity and breeding success models to evaluate the relative importance of conditions at the breeding colony. These comprised rabbit density (a proxy for the degree of degradation of nesting habitat), and extreme rainfall events during early chick-rearing (the number of days in January of rainfall in the 80^{th} percentile of the long-term average, tested on breeding success only).

Results

Model parameters

Poor goodness-of-fit was found for all species; black-browed ($\chi^2_{95} = 154.15$, $p < 0.001$), grey-headed ($\chi^2_{124} = 390.28$, $p < 0.001$), light-mantled ($\chi^2_{219} = 799.70$, $p < 0.001$) and wandering albatrosses ($\chi^2_{187} = 372.84$, $p < 0.001$). For grey-headed and light-mantled albatrosses trap-shyness was detected ($\chi^2_{21} = 221.47$, $z = 10.22$, $p < 0.001$ and $\chi^2_{29} = 381.08$, $z = 15.31$, $p < 0.001$, respectively). The biennial breeding frequency and associated lower breeding propensity of grey-headed and light-mantled albatrosses may explain the trap-shyness detected for these species. Biennial breeding is accounted for by possible transitions into unobservable states. In contrast, trap-happiness was detected for black-browed albatrosses ($\chi^2_{23} = 88.29$, $z = -6.30$, $p < 0.001$). Trap-happiness, is likely an artefact of reduced accessibility for investigators to portions of the study site during periods of high rabbit grazing; consequently, individuals in accessible locations were re-encountered more frequently. Black-browed and wandering albatross encounter histories showed evidence of under-dispersion, which may simply reflect greater uncertainty in the estimation process due to its smaller sample size. To correct for lack of fit to the underlying capture-mark-recapture assumptions, over-dispersion factors ($\hat{c}$) of 0.71, 1.00, 1.46 and 0.51 were included in the models for black-browed, grey-headed, light-mantled and wandering albatrosses, respectively.

Comparative demographic rates

The populations within the Macquarie Island albatross community have differing long-term trends: two species are increasing (black-browed and light-mantled albatrosses), one decreasing (wandering albatrosses) and one is stable (grey-headed albatrosses) (Fig. 3). Of these, black-browed albatrosses had the lowest survival ($\Phi = 0.91 \pm 0.010$) and breeding success ($\gamma = 0.52 \pm 0.02$) probabilities (Table 2) and wandering albatrosses had the lowest breeding propensity ($\beta = 0.74 \pm 0.04$). A negative trend in survival was only evident for wandering albatrosses. Black-browed, grey-headed and wandering albatross breeding propensity decreased during the study period ($\beta = -0.89 \pm 0.23$, $\beta = -1.01 \pm 0.32$ and $\beta = -0.62 \pm 0.22$) (Table S3), while light-mantled albatrosses breeding propensity was constant ($\beta = -0.51 \pm 1.40$). Breeding success of the four species was stable between 1995 and 2014, with no detectable trend (Table S3). No significant correlations in demographic rates amongst species were detected (Table S4).

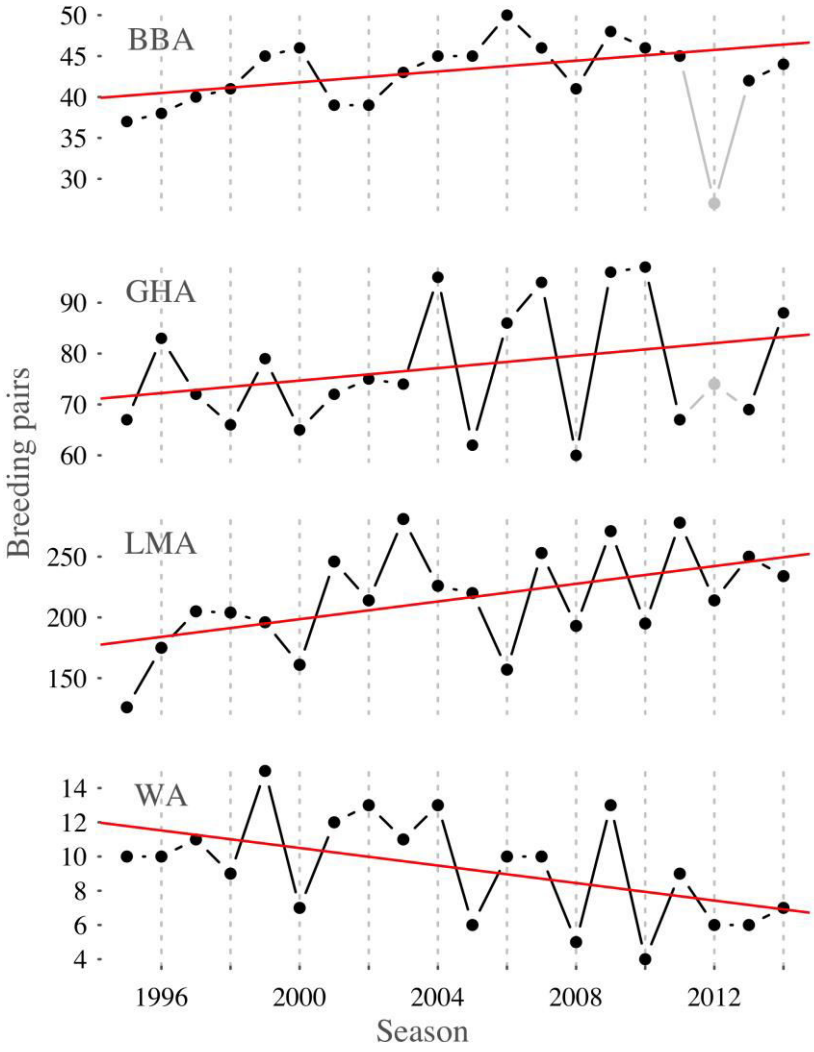

Figure 3 Trends in Macquarie Island black-browed (BBA, $F_{1,17}$=6.88, p=0.018, R^2=0.25), grey-headed (GHA, $F_{1,17}$=1.55, p=0.229, R^2=0.03), light-mantled (LMA, $F_{1,18}$=6.62, p=0.019, R^2=0.23) and wandering albatrosses (WA, $F_{1,18}$=5.84, p=0.027, R^2=0.20) breeding pairs (1995-2014). Note that 1) detection probability of black-browed and grey-headed albatrosses was considerably lower in 2012 than other years and so this point was not included in the linear fit and 2) the number of light-mantled albatross breeding pairs, represent those within seven study sites and approximately ~10% of the total population.

Table 2 Modelled constant demographic estimates for Macquarie Island albatrosses from 1995-2014.

	Survival (ϕ)	Breeding propensity (β)	Breeding success (γ)
Black-browed	0.914 ± 0.010	0.748 ± 0.025	0.516 ± 0.023
Grey-headed	0.925 ± 0.009	0.897 ± 0.033	0.607 ± 0.025
Light-mantled	0.924 ± 0.006	0.988 ± 0.008	0.635 ± 0.030
Wandering	0.939 ± 0.014	0.738 ± 0.039	0.617 ± 0.041

Influence of fisheries on survival

Longline fishing effort in the south-west and the southern Atlantic Ocean and trawl fishing effort in New Zealand waters explained some of the variability in black-browed albatross adult survival. Specifically, Chilean (1995-2009), Falkland and ICCAT longline fisheries

were associated with a decrease in survival, explaining approximately 22–32% of the short- and long-term variability (Fig. 4 & Fig. S2). New Zealand trawl fisheries were positively related to black-browed albatross survival and explained 21.1% of long-term variability (Fig. 4 & Fig. S2). Combined fisheries covariates explained 23.5% of short-term and 45.2% of the long-term variability in survival for this species (Table 3).

Table 3 Time-dependent (*t*) basic and de-trended (*d*) models with combined significant oceanic, fisheries and onshore covariates explaining (%R^2) Macquarie Island albatross demographic rates. Shaded areas represent covariates not considered for each demographic parameter.

			Fisheries	**Oceanic**	**Onshore****	**Global model**
Survival (ϕ)	*Black-browed albatross*	*t*	45.2	10.0		**61.9**
		d	23.5	21.6		**38.8**
	Grey-headed albatross	*t*				
		d		22.6		**22.6**
	Light-mantled albatross	*t*		53.2		**53.2**
		d		53.8		**53.8**
Breeding propensity (β)	*Black-browed albatross*	*t*		75.0*	75.6	**82.7**
		d			33.4	**33.4**
	Grey-headed albatross	*t*		20.5*	31.2	**31.2**
		d				
	Light-mantled albatross	*t*			20.1	**20.1**
		d			31.7	**31.7**
Breeding success (γ)	*Black-browed albatross*	*t*		27.6	33.4	**50.1**
		d		28.5	49.6	**58.3**
	Grey-headed albatross	*t*		29.1		**29.1**
		d		27.2		**27.2**
	Light-mantled albatross	*t*		22.2		**22.2**
		d		33.4		**33.4**

*Confounded by corresponding linear trends in breeding propensity and sea surface height anomaly across the distribution of black-browed and grey-headed albatrosses. **Onshore covariates including rabbit density and extreme rainfall events from Chapter 3.

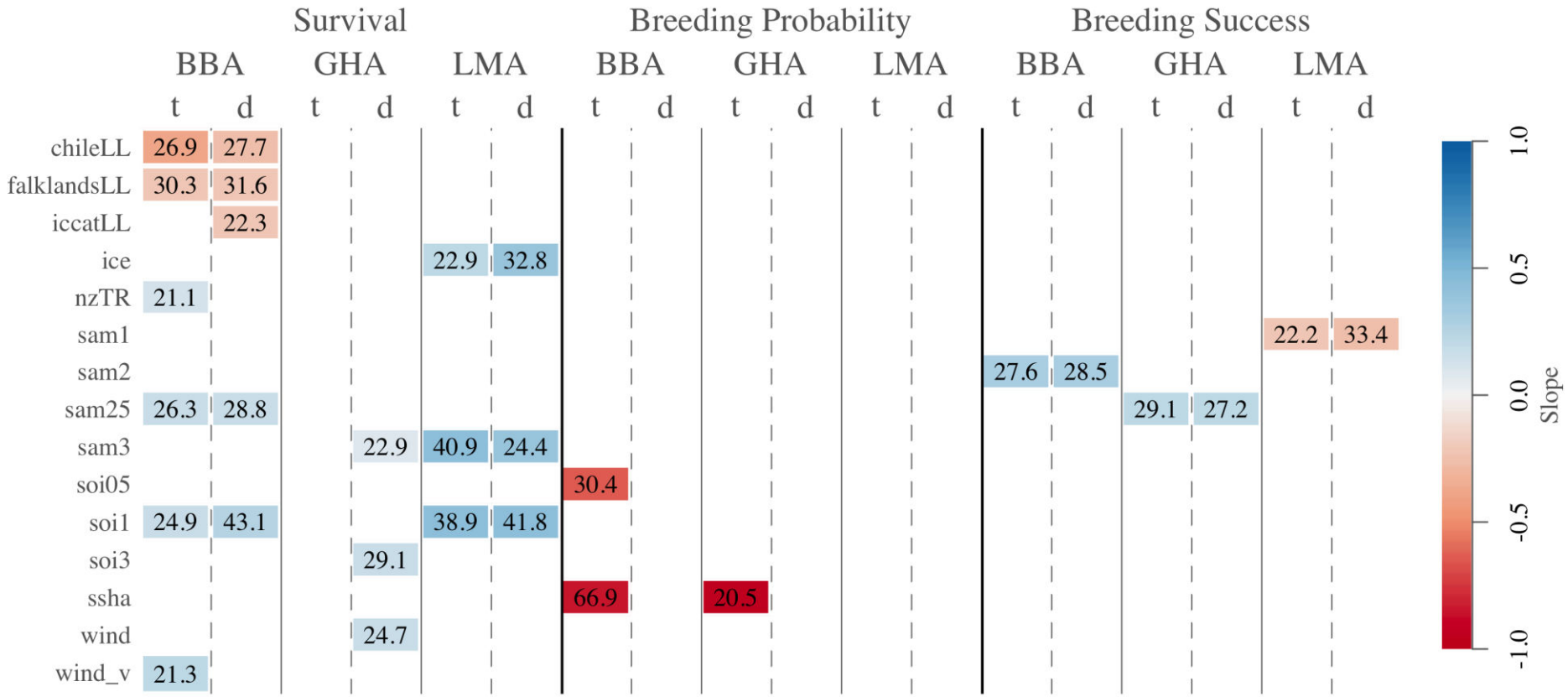

Figure 4 Deviance explained (%R^2) and direction of slope of individual significant fisheries and oceanic covariates (from Table 1) included in survival, breeding propensity and breeding success time-dependent basic (*t*) and linear de-trended (*d*) models of Macquarie Island black-browed (BBA), grey-headed (GHA) and light-mantled (LMA) albatrosses. The definition of acronyms used to describe covariates are contained in Table 1. Numerical suffixes from 05 to 3 indicate the lag applied to the oceanic covariates, from half-yearly (05) to three years (3).

Effect of oceanic factors

Oceanic covariates and large-scale climate indices influenced albatross demographic rates differently among the species. Sea ice extent explained 32.8% and 22.9% of the short and long-term variability in light-mantled albatross survival, with a lower sea ice extent corresponding to increased survival (Fig. 4 & Fig. S4). Increased meridional wind (southerly winds) and higher wind speeds were associated with higher survival of black-browed albatrosses (Fig. 4 & Fig. S2) and grey-headed albatrosses (Fig. 4 & Fig. S3), respectively. Sea surface height anomaly explained 66.9% and 20.5% of the long-term variability in black-browed and grey-headed albatross breeding propensity. This correlation is not particularly informative and appears to be a result of strong linear trends in both breeding propensity and sea surface height anomaly, but without any obvious mechanism linking the two (Fig. 4 & Fig. S5-6).

The SOI and SAM were positively associated with survival for all three species, with varying temporal lags. With a three-year lag, the SAM explained 22.9% of the short-term variability in grey-headed albatross survival and 24.4% and 40.9% of the short-term and long-term variability in light-mantled albatross survival (Fig. 4 & Fig. S3-4). With a shorter two and a half-year lag, the SAM explained 28.8% and 26.3% of the short and long-term variability, respectively in black-browed albatross survival (Fig. 4 & Fig. S2). Breeding success of black-browed and grey-headed albatross showed a positive association with higher SAM with two and two and a half-year lags (Fig. 4 & Fig. S8-9). In contrast, light-mantled albatross breeding success was negatively associated with higher SAM indices after a one-year lag (Fig. 4 & Fig. S10).

There was a positive association between SOI and survival for all species (Fig. 4). For black-browed and light-mantled albatross survival, the response to higher SOI values occurred with a one-year lag and explained 43.1% and 41.8% of the short-term variability and 24.9% and 38.9% of the long-term variability, respectively (Fig. 4 & Fig. S2, S4). Grey-headed albatrosses responded more slowly, with a three-year lag, explaining 29.1% of short-term variability (Fig. 4 & Fig. S3). Black-browed albatross breeding propensity was negatively related to SOI with a six-month lag, describing 30.4% of variability (Fig. 4 & Fig. S5).

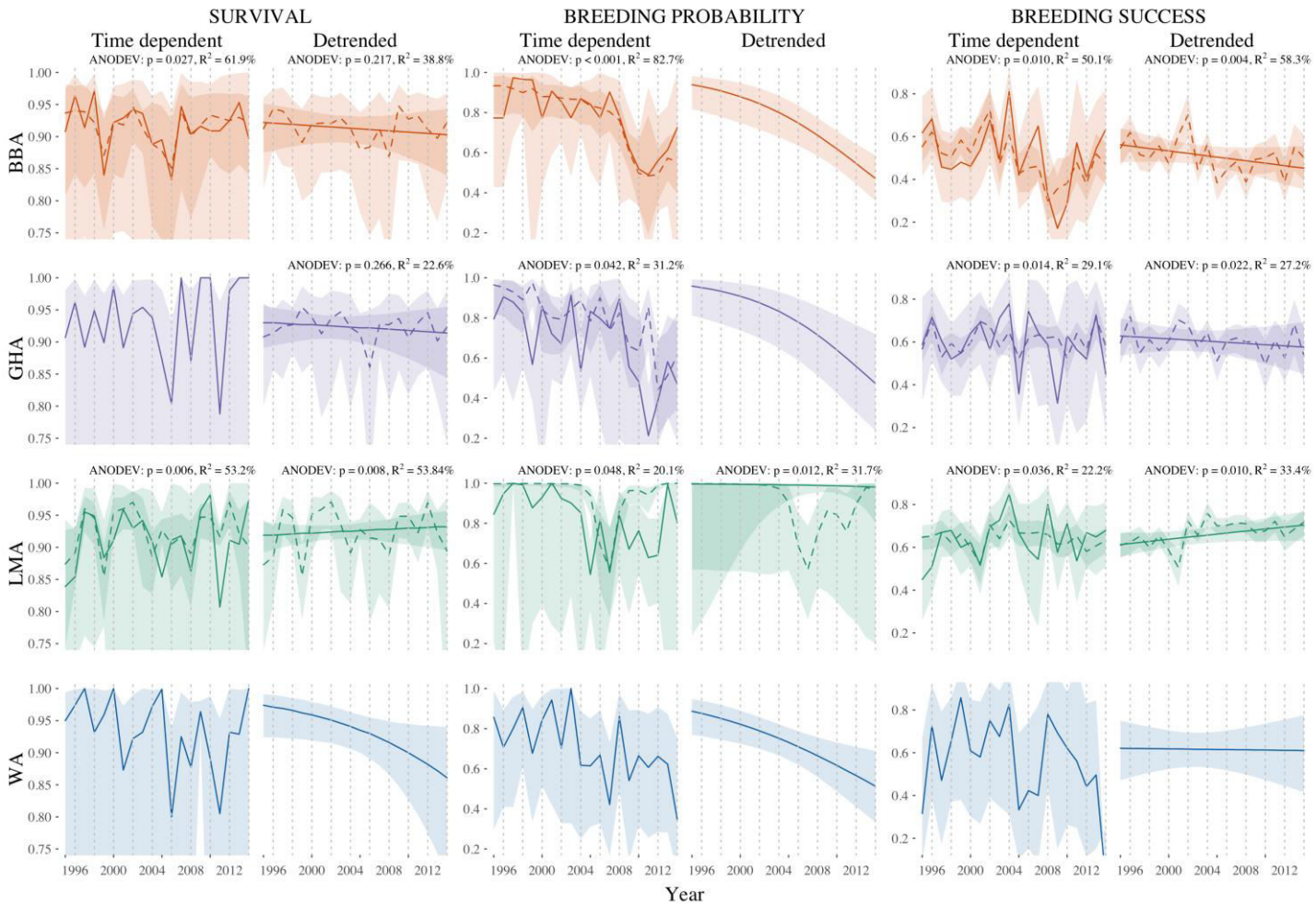

Figure 5 Global integrated models showing annual variation in demographic rates of adult black-browed (BBA, orange), grey-headed (GHA, purple) and light-mantled (LMA, green) albatrosses at Macquarie Island, modelled as time-dependent and linear de-trended (solid coloured lines) and as a function of combined significant covariates (broken coloured lines) including 0.95 confidence intervals. Detailed results for each species, trait and covariate are contained in Fig. S2-10.

The most influential atmospheric, oceanographic and climate covariates were combined in a model for each species and each demographic parameter (Table 3). The combined oceanic variables described 53.8% and 53.2% of the short and long-term variation in light-mantled albatross survival. Oceanic factors were not strongly correlated with black-browed albatross survival (short-term variability: R^2 = 21.6%, long-term variability: R^2 = 10.0%) or grey-headed albatross survival (short-term variability: R^2 = 22.6%). Combined sea surface height anomaly and SOI (six-month lag) comprised the oceanic factors that explained 75.0% of the long-term variability in breeding propensity of black-browed albatrosses. The remaining significant demographic models tested against oceanic factors included only a single variable.

Global models and onshore effects

Global models integrated all influential fisheries and oceanic covariates, as well as onshore breeding habitat quality predictors from Chapter 3 (Table 3 & Fig. 5). Habitat degradation caused by heavy rabbit grazing was strongly correlated with the breeding propensity of all three species. For black-browed albatrosses, heavy January rainfall and high rabbit density at the breeding colony explained 49.6% and 33.4% of the short-term and long-term variability in breeding success. Fisheries and oceanic variables best explained the variability seen in black-browed albatross survival, whereas fisheries, oceanic and onshore variables best explained black-browed albatross survival and breeding success. The remaining global models were almost exclusively oceanic factors for survival and breeding success and onshore factors for breeding propensity.

Discussion

Understanding the extrinsic drivers of demographic variability is critical to assess population viability, particularly in small populations where small decreases in vital rates can have a considerable impact on the population. However, the natural demographic stochasticity of small populations can make it challenging to identify the key factors contributing to demographic variability.

Species-specific demographic estimates

Notwithstanding the overall similarity in survival patterns, there were also important species-specific differences. Mean adult survival of black-browed albatrosses was constant throughout the study period, continuing the pattern reported between 1975-2000 (Terauds et al., 2005). While survival was lower than in the other albatross species at Macquarie Island, the mean was similar to values for this species from Isles Kerguelen (Weimerskirch and Jouventin, 1998, Nevoux et al., 2007, Rolland et al., 2008, Pardo et al., 2013), South Georgia (Prince et al., 1994, Croxall et al., 1998, Arnold et al., 2006, Pardo et al., 2017) and the Falkland Islands (Catry et al., 2011). In contrast, breeding success was higher than at South Georgia (Croxall et al., 1998) and some colonies at the Falkland Islands (ACAP, 2009), potentially reflecting reduced density dependent constraints at Macquarie Island.

Survival in grey-headed albatross at Macquarie Island varied little over time (92.5 ± 0.01%, 1995-2014), but was considerably lower than the long-term average from South Georgia of 96.0 ± 0.1% (Prince et al., 1994, Pardo et al., 2017), where the population is in rapid decline (Poncet et al., 2017), at Campbell Island (95.3 ± 0.9%; Waugh et al., 1999b) and Marion Island (95.1 ± 0.0%; Converse et al., 2009). In contrast, breeding success for the Macquarie Island population (60.7 ± 2.5%) is higher than Campbell Island (39.7%) (Waugh et al., 1999b) and almost double that of the South Georgia population (Pardo et al., 2017). Estimates of grey-headed albatross survival are highly variable in the Southern Ocean, suggesting that factors that influence survival may originate from local or regional sources such as density-dependent processes and individual fisheries.

The cryptic coloration of light-mantled albatross, dispersed distribution of nests, and difficulty in accessing sites on cliffs and steep slopes is such that there are few capture-mark-recapture studies of this species (Schoombie et al., 2016). Survival of Macquarie Island light-mantled albatrosses at Macquarie Island (92%, 1995-2014) was considerably lower than at the Crozet Isles (97.3%, 1967-1995), whereas breeding success was higher at Macquarie (63.5% in 1995-2014 vs 40.9% in 1980-2005 at Crozet (Weimerskirch and Jouventin, 1998, Delord et al., 2008). The slight positive trend over time in adult survival may explain the increase in breeding pairs at Macquarie Island. However, a comparison between historical field sketches (1994-98) and current GPS locations indicate that the extent of the study areas might have reduced over time, reducing resighting probabilities of individuals marked in the

early years. If this contraction has occurred, it would likely weaken the ability to detect trends in demographic parameters.

The wandering albatross population on Macquarie Island has declined to an average of only five breeding pairs each year (DPIPWE, 2014). Their long-term persistence seems unlikely given the negative trend in adult survival and breeding propensity and the negligible recruitment by nonbreeding immigrants (Terauds et al., 2006b). The decline in breeding propensity may be amplified by reduced survival, as it will be more difficult for widowed birds to find a new mate, particularly given the strong male-biased sex ratio (Fig. S11) (DPIPWE, 2014). Due to the small population size we could not test for relationships between vital rates and fisheries effort or oceanographic change, but the decline of wandering albatross on Macquarie Island has previously been linked to tuna longline fisheries (de la Mare and Kerry, 1994). Nonetheless, this population has recovered from critically low numbers in the past. Harvesting by humans in the 18th century reduced the population to one or two breeding pairs in 1911 (Cumpston, 1968). Subsequently the number of breeding pairs fluctuated from 28 in 1968 to two in 1985 before recovering to 15 in 1999 (Terauds et al., 2006b). The Amsterdam albatross *Diomedea amsterdamensis* increased from five to 31 breeding pairs between 1983 and 2001 (Weimerskirch et al., 1997a, Rivalan et al., 2010). Indeed, recovery capacity may not be constrained by genetic bottlenecks, as albatrosses in general show surprisingly low genetic variation (Milot et al., 2007).

Influence of fisheries on survival

Bycatch in longline and trawl fisheries is the greatest contributor to declines in albatross populations in the Southern Ocean (Gales and Robertson, 1998, Phillips et al., 2016), although prior to our study there was no apparent evidence of its impact on black-browed albatrosses at Macquarie Island (Terauds et al., 2005). Our study, based on a longer time series found a relationship between fisheries effort and survival only in the black-browed albatross, with higher mortality rates associated with greater longline effort in the south-west Atlantic, a known wintering region for this population (Chapter 2). Bycatch mortality in fisheries without mitigation measures in this region range from of 0.03 to 0.05 birds per 1000 hooks in the Chilean artisanal hake *Merluccius australis* and toothfish fisheries to 0.276 in the Uruguayan tuna fleet (Moreno et al., 2006, ICCAT, 2010, Jiménez et al., 2010, Yeh et al., 2013). Effort in some fisheries, including those within the Argentinean EEZ, were not publically available and so could not be included in our models. High levels of black-browed

albatross bycatch occur in Argentinean longline fisheries, with estimates of 0.010 ± 0.001 birds per 1000 hooks caught between 2001-2010 (Favero et al. 2013). The negative relationship between black-browed albatross survival and southwest Atlantic fisheries seems likely to reflect a direct causal link because this is a known wintering region for the Macquarie Island population (Chapter 2), and high bycatch rates of black-browed albatrosses have been reported there previously (Favero et al., 2013, Yeh et al., 2013).

Survival of Macquarie Island black-bowed albatrosses was also related to effort the New Zealand trawl fisheries, but with higher effort associated with increased survival. Black-browed albatross bycatch within these fisheries is low (0.05 captures per 100 tows per year) (Abraham and Thompson, 2015). Furthermore, they are known scavengers of fisheries discards within the subantarctic area of the New Zealand trawl fisheries attending squid trawlers in high numbers during pre-laying and early incubation (Petyt, 1995). Higher breeding success at Isles Kerguelen was attributed to the availability of discards during periods of high fishing effort (Rolland et al., 2008). New Zealand Trawl fisheries potentially supported the long-term survival of Macquarie Island black-browed albatrosses by providing a nearby resource that improved body condition. The short-term influence of discards on survival may be harder to detect than bycatch related mortality, due to the complex processes associated with allocation of energy resources.

Effect of oceanic factors

Both the SAM and SOI are predicted to influence seabird demography and hence population viability by modifying ocean circulation patterns, which in turn influences primary production (Trathan et al., 2007). Furthermore, changes in the intensity and positioning of Southern Ocean wind regime, associated with the SAM, can have a more direct effect on demographic rates by influencing the energetic cost of flight and therefore of foraging (Weimerskirch et al., 2012). The demographic rates of Macquarie Island albatrosses were correlated with the SAM and the SOI. The SAM influences Southern Ocean wind patterns and has complex and lagged effects on physical oceanography and biological productivity (Marshall, 2003, Lefebvre and Goosse, 2005). Higher values for the SAM index is associated with fluctuations in penguin populations in the east Antarctic (Ainley et al., 2005), reduced krill densities at South Georgia (Fielding et al., 2014) and improved maternal condition of southern elephant seals *Mirounga leonina* at Macquarie Island (McMahon et al., 2017). However, the underlying mechanisms and ecological consequences are not clear, especially

for wide-ranging species such as albatrosses. High SAM indices correspond to stronger winds closer to the pole and were associated with increased survival of Macquarie Island black-browed, grey-headed and light-mantled albatrosses and with increased breeding success of black-browed and grey-headed albatrosses following a two to three-year lag. During positive phases of the SAM, waters within the Antarctic Zone have colder sea surface temperatures, increased iron supply and upwellings, supporting higher surface chlorophyll. In contrast, in the Subantarctic Zone, a deeper mixed layer results in reduced surface productivity (Lovenduski and Gruber, 2005). Surface productivity in the Antarctic Zone is transported to lower latitudes through Ekman processes (Lovenduski and Gruber, 2005) and may provide better foraging for Macquarie Island albatrosses after a two to three-year lag. Positive SAM indices also lead to increased eddy kinetic energy following a two to three-year lag, due to the time taken for stronger wind forcing to influence the Antarctic Circumpolar Current (Meredith and Hogg, 2006). Nonbreeding black-browed and grey-headed and breeding light-mantled albatrosses utilise regions of higher eddy kinetic energy (Chapter 2), which act as prey-aggregating systems (Bost et al., 2009, Scales et al., 2014). Nutrient retention and enrichment of surface waters through upwelling and mixing at mesoscale cyclonic eddy features support higher phytoplankton and prey concentrations relative to surrounding waters (Mitchell et al., 1991, Sokolov and Rintoul, 2007).

In contrast, light-mantled albatross breeding success was negatively associated with SAM indices after a one-year lag. Breeding light-mantled albatrosses forage along the Subantarctic Front near Macquarie Island and in Antarctic waters (~65°S) south of Macquarie Island (Chapter 2). They have the most southerly breeding distribution of all Macquarie Island species, which may make them responsive to variability in sea ice concentration and primary productivity occurring on shorter timescales, although the proximal mechanisms are unclear. Further, survival was negatively related to sea ice extent, which may represent an increase in potential foraging habitat at high latitudes for this species. Similarly, fewer female southern elephant seals breed on Macquarie Island following years of increased sea ice duration due to exclusion from high quality habitat and prey resources (van den Hoff et al., 2014).

The positive response of black-browed and grey-headed albatross survival to more southerly and greater wind speeds, respectively, may be due to the influence of wind patterns on the energetics of flight. The relatively high wing loading of grey-headed albatrosses means that stronger winds improve flight efficiency by increasing glide ratios and reducing the cost of

reaching foraging areas (Pennycuick, 1982, Phillips et al., 2004). For black-browed albatrosses, more southerly winds would act in a similar way, supporting efficient northward flight to foraging areas. The direct effect of wind parameters on survival has been found in very few and recent studies (Pardo et al., 2017). These results suggest that the predictions of increasingly positive SAM and subsequent strengthening of southerly circumpolar winds may be beneficial to black-browed and grey-headed albatrosses, although not for light-mantled albatrosses breeding on Macquarie Island. There were similar responses to wind patterns for wandering albatrosses in the south Indian Ocean, where body condition and breeding success improved with increasing wind speed and meridional wind, related to the SAM (Weimerskirch et al., 2012). Furthermore, Pardo et al. (2017) showed a strong positive effect of wind patterns on adult and juvenile survival of wandering albatrosses at South Georgia.

A positive relationship between SOI and survival was detected in the three species of albatrosses at Macquarie Island for which sufficient data were available. Positive SOI (La Niña) periods are associated with higher productivity in the eastern Pacific boundary currents (Barber and Chavez, 1983, Behrenfeld et al., 2001) and are associated with improved hatching success of Indian yellow-nosed albatrosses *Thalassarche carteri* from Amsterdam Island and breeding success of black-browed albatrosses from Isles Kerguelen (Rolland et al., 2008, Rolland et al., 2009). A positive SOI may enhance biological productivity and increase recruitment of mid-trophic prey species (Waluda et al., 1999). El Niño conditions in the Pacific sector covaried positively with a negative SAM during our study period, making it difficult to disentangle the influence of these two large-scale climate cycles (Stammerjohn et al., 2008). Despite this, future predictions indicate increasing frequency of extreme El Niño events due to anthropogenic climate change (Cai et al., 2014), which may reduce the survival of albatrosses at Macquarie Island.

Global models and onshore effects

Nesting habitat quality (indicated by rabbit density) was the most influential determinant of the breeding propensity of the three species. This is most likely due to overgrazing of vegetation and subsequent slope erosion associated with high rabbit densities. Environmental conditions that influence seabird breeding are commonly those that affect pre-breeding body condition, such as oceanographic conditions that influence prey availability (Barbraud and Weimerskirch, 2005, Lee et al., 2007). The high correlation between breeding propensity and rabbit density dominated the models, swamping other potential environmental drivers. The

effects of rabbit density and heavy rainfall events at the colony explained 49.6% of the short-term variation in breeding success of black-browed albatrosses, whereas oceanic factors, accounted for 28.5% of the short-term variation. Fisheries effort best explained adult survival for this species. Therefore, for the black-browed albatross, changes in fisheries and breeding habitat quality had the greatest influence on survival, breeding propensity and breeding success; factors for which mitigation strategies already exist (Croxall et al., 2012). The removal of rabbits from Macquarie Island (Springer, 2016) and current bycatch mitigation in the south-west Atlantic (Barton, 2002, Otley et al., 2007, Moreno et al., 2008) may, therefore, offer an explanation for the increasing population of black-browed albatrosses on Macquarie Island. For the remaining species, the results are less conclusive and options for management less obvious. For both grey-headed and light-mantled albatrosses, processes on land had a significant effect on breeding propensity, and so the recent removal of rabbits from Macquarie Island should improve reproductive output. There are, however, few options to mitigate climate effects on their survival and breeding success.

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Supporting Information

Table S1 Summary table of encountered wandering albatrosses on Macquarie Island according to state from 1994/95 to 2014/15.

		Successful breeders	Failed breeders	Breeders with unknown breeding outcome	Nonbreeders	Total
Wandering albatross	1994/95	12	8	0	19	39
	1995/96	6	13	0	17	36
	1996/97	16	6	0	21	43
	1997/98	8	10	0	21	39
	1998/99	20	10	0	17	47
	1999/00	12	2	0	25	39
	2000/01	14	10	0	19	43
	2001/02	14	12	0	15	41
	2002/03	15	7	0	17	39
	2003/04	19	7	0	15	41
	2004/05	8	4	0	17	29
	2006/07	8	12	0	18	38
	2007/08	8	12	0	19	39
	2008/09	4	7	0	27	38
	2009/10	20	7	2	8	37
	2010/11	5	2	1	14	22
	2011/12	10	8	0	17	35
	2012/13	12	0	0	14	26
	2013/14	6	6	0	10	22
	2014/15	8	6	0	21	35

Table S2 Input GEMACO sentences for the time-dependent model analysis in E-Surge. t refers to time and f refers to previous breeding state, 1 to 63 refers to time periods 1952 to 2015 + others accounts for the parameters not accounted for in the main sentence, i stands for constant (refer to E-Surge manual). Seasons 1994/95 to 2014/15 correspond time steps 43 to 63 and are the subject of the analysis.

		Black-browed	Grey-headed	Light-mantled	Wandering
Initial state (i)		i	i	i	i
Transition (ψ)	Survival (ϕ)	t(1:42) + t(43_63)	t(1:42) + t(43_63)	t(1:42) + t(43_63)	t(1:42) + t(43_63)
	Return (r)	t(1:42) + t(43_63)	[t(43_63) + f(1,2 3 4 5 6)] + others	[t(43_63) + f(1,2 3 4 5 6)] + others	[t(43_63) + f(1,2 3 4 5 6)] + others
	Breeding (β)	t(1:42) + t(43_63)	[t(43_63) + f(1,3 5 7 8 9)] + others	[t(43_63) + f(1,3 5 7 8 9)] + others	[t(43_63) + f(1,3 5 7 8 9)] + others
	Breeding success (γ)	t(1:42) + t(43_63)	t(1:42) + t(43_63)	t(1:42) + t(43_63)	t(1:42) + t(43_63)
Event (Ω)	Detection (p)	firste + nexte.[t(43_63) + f(1 2,3)] + others	firste + nexte.[t(1:42) + f(1 2,3).[i + t(43_62) * rabbit $_{lag2.5}$]]	firste + nexte.[f.[t(1:42) + [i + t(43_62) * rabbit $_{lag1.5}$]]]	firste + nexte.[t(43_63) + f(1 2,3)] + others
	Breeding outcome uncertainty (k)	i	i	i	i

Table S3 Multi-event capture-recapture modelling of black-browed, grey-headed and light-mantled albatrosses at Macquarie Island, testing the influence of fisheries and oceanic on survival, breeding propensity and breeding success from 1994-2015. Habitat covariates (extreme rainfall events, *rain* and rabbit density, *rabbits*) included in the global integrated models are from Chapter 3.

	Model	Np	Deviance	pANODEV	R^2 (%)	slope	SE
	Black-browed albatross						
	cst	1	5882.84				
	t	20	5868.71				
	t + lin	2	5882.32	0.421	3.62	-0.07	0.15
	t + chileLL	2	5879.03	**0.019**	26.93	-0.36	0.28
	t + lin + chileLL	3	5878.55	**0.021**	27.71	-0.22	0.16
	t + falklandsLL	2	5878.56	**0.012**	30.27	-0.21	0.15
	t + lin + falklandsLL	3	5878.03	**0.012**	31.56	-0.21	0.15
	t + iccatLL	2	5882.27	0.399	3.98	0.08	0.16
	t + lin + iccatLL	3	5879.29	**0.041**	22.27	-0.18	0.16
	t + nzTR	2	5879.86	**0.042**	21.10	0.17	0.14
	t + lin + nzTR	3	5879.65	0.058	19.61	0.16	0.15
	$t + sam_{lag2.5}$	2	5879.13	**0.021**	26.27	0.21	0.16
	$t + lin + sam_{lag2.5}$	3	5878.41	**0.018**	28.77	0.21	0.16
	$t + soi_{lag1}$	2	5879.33	**0.025**	24.85	0.21	0.17
	$t + lin + soi_{lag1}$	3	5876.45	**0.002**	43.12	0.28	0.17
	t + wind_v	2	5879.83	**0.041**	21.28	0.25	0.23
	t + lin + wind_v	3	5879.68	0.059	19.46	0.24	0.23
	t + chileLL+ falklandsLL+ nzTR	4	5876.46	**0.020**	45.16		
	t + lin + chileLL+ falklandsLL + iccatLL	5	5879.12	0.246	23.51		
	$t + sam_{lag2.5} + soi_{lag1} +$ *wind_v*	4	5881.42	0.628	10.02		
	$t + lin + sam_{lag2.5} + soi_{lag1}$	4	5879.381	0.142	21.62		
Survival (ϕ)	t + *chileLL+ falklandsLL+ nzTR* + $sam_{lag2.5} + soi_{lag1}$ + *wind_v*	7	5874.10	**0.027**	61.87		
	t + lin + chileLL+ falklandsLL+ iccatLL + $sam_{lag2.5} + soi_{lag1}$	7	5877.046	0.217	38.8		
	Grey-headed albatross						
	cst	1	10024.75				
	t	20	10000.70				
	t + lin	2	10024.29	0.559	1.93	-0.07	0.17
	$t + sam_{lag3}$	2	10023.30	0.295	6.06	0.13	0.23
	$t + lin + sam_{lag3}$	3	10018.84	**0.038**	22.87	0.13	0.23
	$t + soi_{lag3}$	2	10024.01	0.458	3.10	0.10	0.23
	$t + lin + soi_{lag3}$	3	10017.36	**0.017**	29.14	0.18	0.25
	t + wind	2	10023.31	0.297	6.01	0.15	0.27
	t + lin + wind	3	10018.40	**0.030**	24.73	0.18	0.28
	$t + lin + sam_{lag3} + soi_{lag3} +$ *wind*	4	10018.9	0.266	22.60		
	Light-mantled albatross						
	cst	2	29149.72				
	t	20	29068.52				
	t + lin	2	29140.84	0.154	10.94	0.06	0.11
	t + ice	2	29131.16	**0.033**	22.86	0.23	0.15
	t + lin + ice	3	29117.09	**0.010**	32.84	0.41	0.18
	$t + sam_{lag3}$	2	29116.51	**0.002**	40.91	0.45	0.18
	$t + lin + sam_{lag3}$	3	29123.23	**0.032**	24.35	0.41	0.18
	$t + soi_{lag1}$	2	29118.12	**0.003**	38.91	0.44	0.16
	$t + lin + soi_{lag1}$	3	29110.58	**0.003**	41.84	0.46	0.17
	$t + ice + sam_{lag3} + soi_{lag1}$	4	29106.54	**0.006**	53.18		
	$t + lin + ice + sam_{lag3} +$	5	29101.90	**0.008**	53.84		

		soi_{lag1}						
	Wandering albatross							
		cst	1	5768.197				
		t	20	5740.776				
		t + lin	2	5759.915	**0.012**	30.20	-0.56	0.29
Breeding propensity (β)	*Black-browed albatross*							
		cst	1	5958.20				
		t	20	5868.71				
		t + lin	2	5893.55	**<0.001**	72.24	-0.89	0.23
		$t + soi_{lag0.5}$	2	5931.02	**0.012**	30.38	-0.64	0.17
		$t + lin + soi_{lag0.5}$	3	5890.25	0.125	13.29	-0.25	0.18
		t + ssha	2	5898.35	**<0.001**	66.88	-0.85	0.21
		t + lin + ssha	3	5890.96	0.178	10.43	0.18	0.17
		$t + soi_{lag0.5}$ + *ssha*	3	5891.12	**<0.001**	74.96		
		$t + soi_{lag0.5}$ + *ssha* + $rabbits_{lag4.5}$	4	5884.21	**<0.001**	82.68		
	Grey-headed albatross							
		cst	1	10142.67				
		t	20	10026.52				
		t + lin	2	10107.72	**0.012**	30.09	-1.01	0.32
		t + ssha	2	10118.92	**0.045**	20.45	-0.92	0.35
		t + lin + ssha	3	10096.88	0.124	13.35	0.33	0.17
		t + ssha + $rabbits_{lag4.5}$	4	10106.43	**0.042**	31.2		
	Light-mantled albatross							
		cst	1	29115.48				
		t	20	29068.65				
		t + lin	2	29114.79	0.611	1.47	-0.51	1.40
		$t + rabbits_{lag0.5}$	2	29106.33	**0.048**	20.10	-2.13	0.40
		$t + lin + rabbits_{lag0.5}$	3	29100.17	**0.012**	31.70	-1.30	0.70
	Wandering albatross							
		cst	1	5834.704				
		t	20	5780.756				
		t + lin	2	5816.067	**0.006**	34.55	-0.62	0.22
Breeding success (γ)	*Black-browed albatross*							
		cst	1	5956.90				
		t	20	5868.71				
		t + lin	2	5952.86	0.365	4.58	-0.14	0.10
		$t + sam_{lag2}$	2	5932.53	**0.017**	27.63	0.31	0.10
		$t + lin + sam_{lag2}$	3	5928.87	**0.019**	28.50	0.31	0.10
		$t + sam_{lag2} + rabbits_{lag3.5}$ + *rainfall*	4	5912.70	**0.010**	50.12		
		$t + lin + sam_{lag2} + rabbits_{lag3.5}$ + *rainfall*	5	5903.79	**0.004**	58.31		
	Grey-headed albatross							
		cst	1	10088.23				
		t	20	10000.7				
		t + lin	2	10085.24	0.435	3.42	-0.07	0.12
		$t + sam_{lag2.5}$	2	10062.80	**0.014**	29.05	0.25	0.11
		$t + lin + sam_{lag2.5}$	3	10062.22	**0.022**	27.23	0.26	0.11
	Light-mantled albatross							
		cst	1	29210.58				
		t	20	29068.52				
		t + lin	2	29203.02	0.328	5.32	0.13	0.08
		$t + sam_{lag1}$	2	29179.06	**0.036**	22.19	-0.19	0.06
		$t + lin + sam_{lag1}$	3	29158.05	**0.010**	33.44	-0.22	0.06

Wandering albatross						
	cst	1	5783.456			
	t	20	5740.776			
	t + lin	2	5783.443	0.942	0.03	-0.01	0.19

* Terms are N_p, the number of structural parameters, ANODEV, analysis of deviance (Grosbois et al., 2008), R^2, the proportion of variance explained by the test covariate. Models *cst*, *t*, *lin,* correspond to constant, time-dependent and linear trend models tested on reproductive rates of survival (ϕ), breeding propensity (β) and breeding success (γ).

Table S4 Correlation coefficients of bootstrapped demographic rates.

		Black-browed	Grey-headed	Light-mantled	Wandering
Survival (ϕ)	Black-browed		0.07	0.02	0.03
	Grey-headed	0.07		0.15	0.22
	Light-mantled	0.02	0.15		0.06
	Wandering	0.03	0.22	0.06	
Breeding propensity (β)	Black-browed		0.31	0.18	0.14
	Grey-headed	0.31		0.21	0.31
	Light-mantled	0.18	0.21		0.3
	Wandering	0.14	0.31	0.3	
Breeding success (γ)	Black-browed		0.3	-0.05	-0.07
	Grey-headed	0.3		0.04	0.15
	Light-mantled	-0.05	0.04		0.16
	Wandering	-0.07	0.15	0.16	

NOTE: No significant correlations were detected i.e. no correlations significantly different from 0.

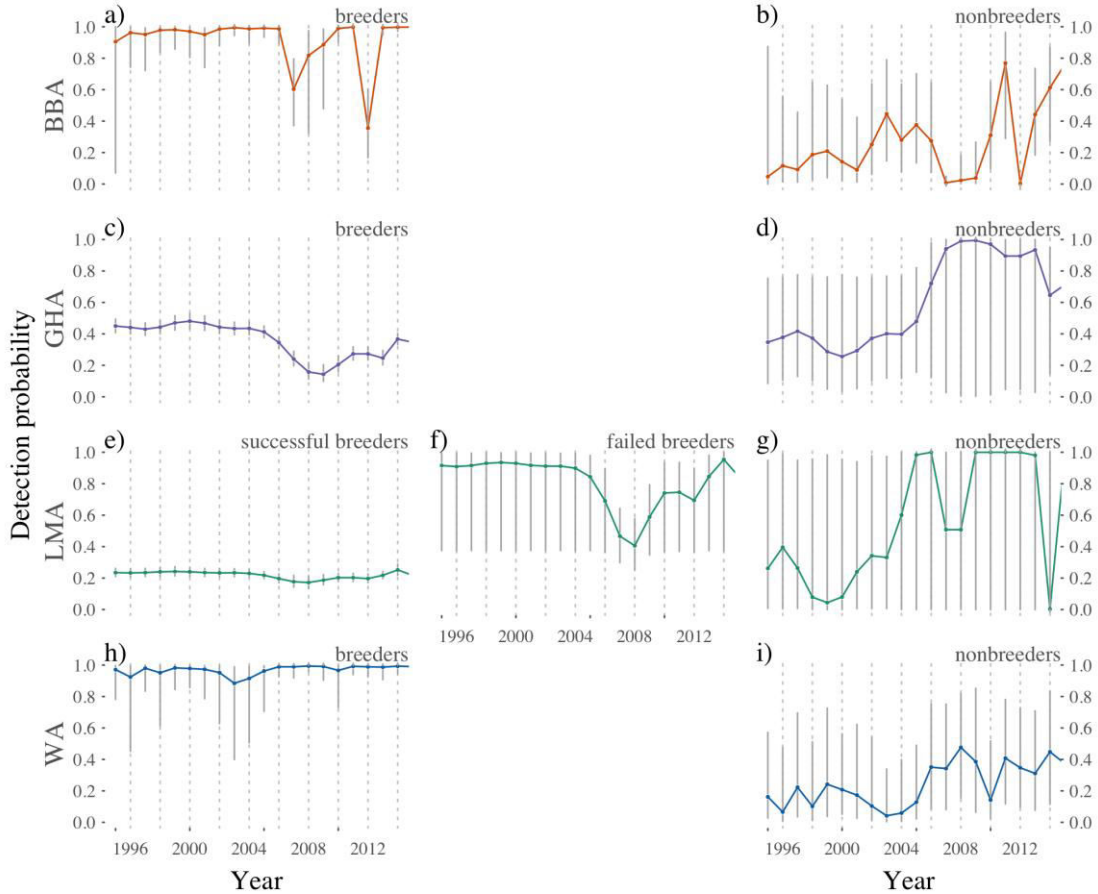

Figure S1 Annual variation in detection probability of experienced adult breeders at Macquarie Island (black-browed, BBA, orange; grey-headed, GHA, purple; light-mantled, LMA, green; and wandering albatrosses, WA, blue), modelled as time-dependent (solid coloured lines) and grouped by breeding status (including successful and failed breeders for light-mantled albatrosses).

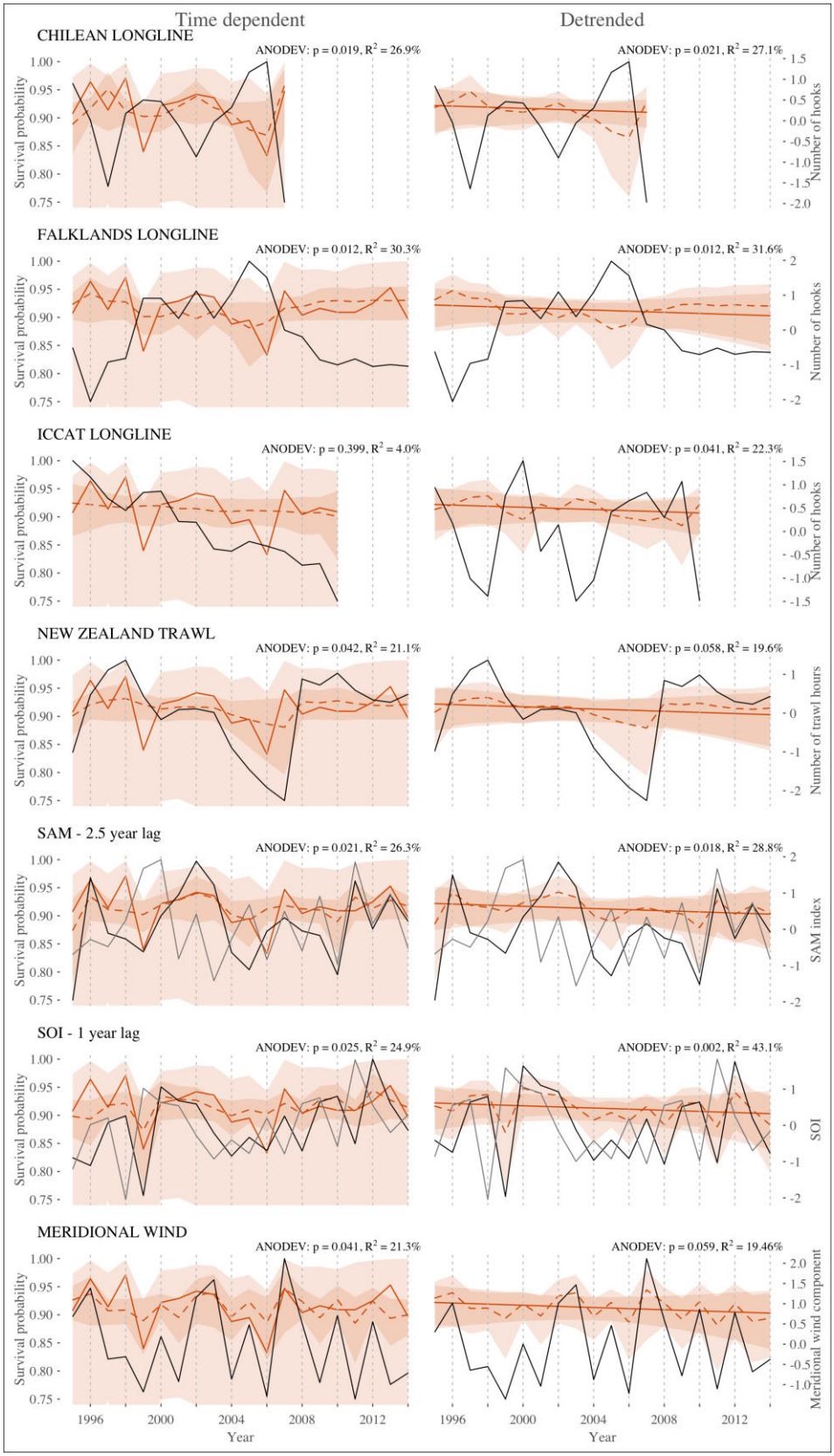

Figure S2 Annual variation in survival probabilities of adult black-browed albatrosses at Macquarie Island, modelled as time-dependent and linear de-trended (solid coloured lines) and as a function of the covariates (broken coloured lines) including 0.95 confidence intervals with standardised covariates (solid black lines), and temporal lags (solid grey lines).

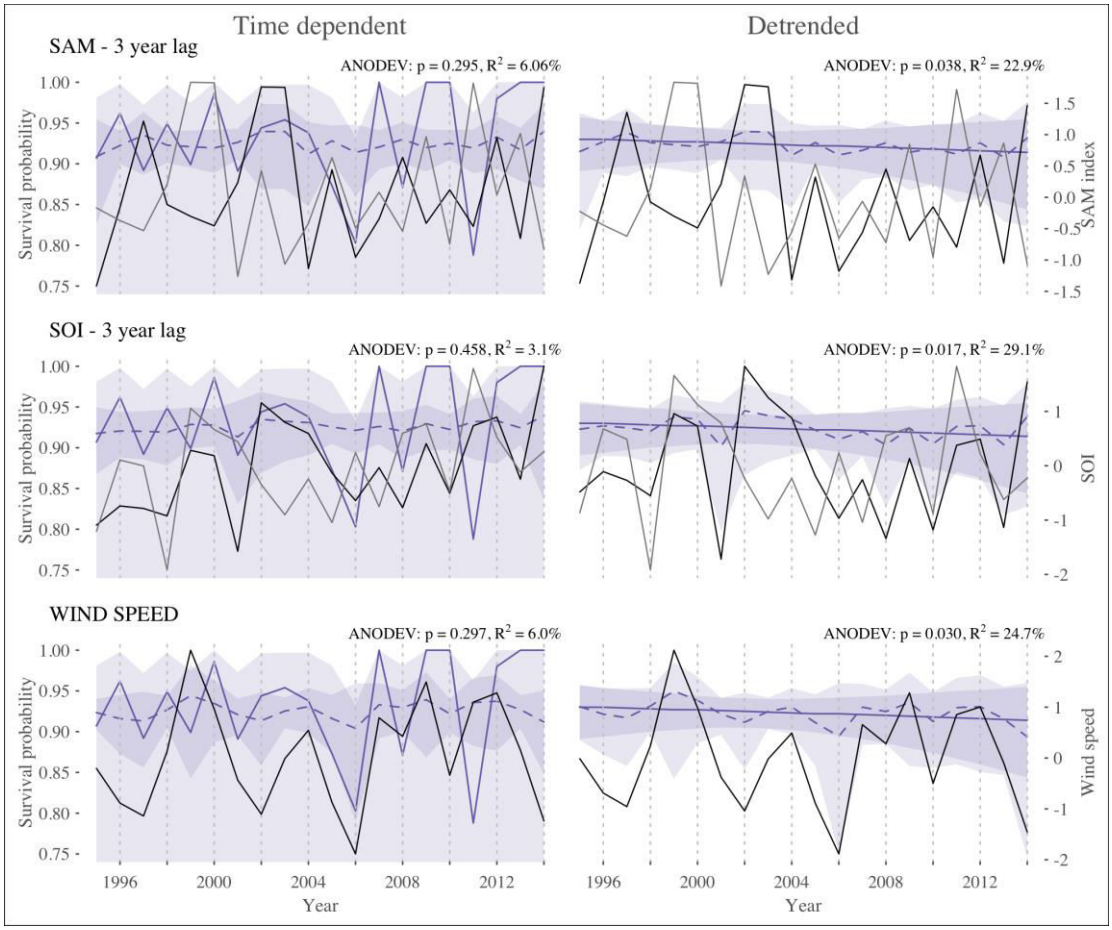

Figure S3 Annual variation in survival probabilities of adult grey-headed albatrosses at Macquarie Island, modelled as time-dependent and linear de-trended (solid coloured lines) and as a function of the covariates (broken coloured lines) including 0.95 confidence intervals with standardised covariates (solid black lines), and temporal lags (solid grey lines).

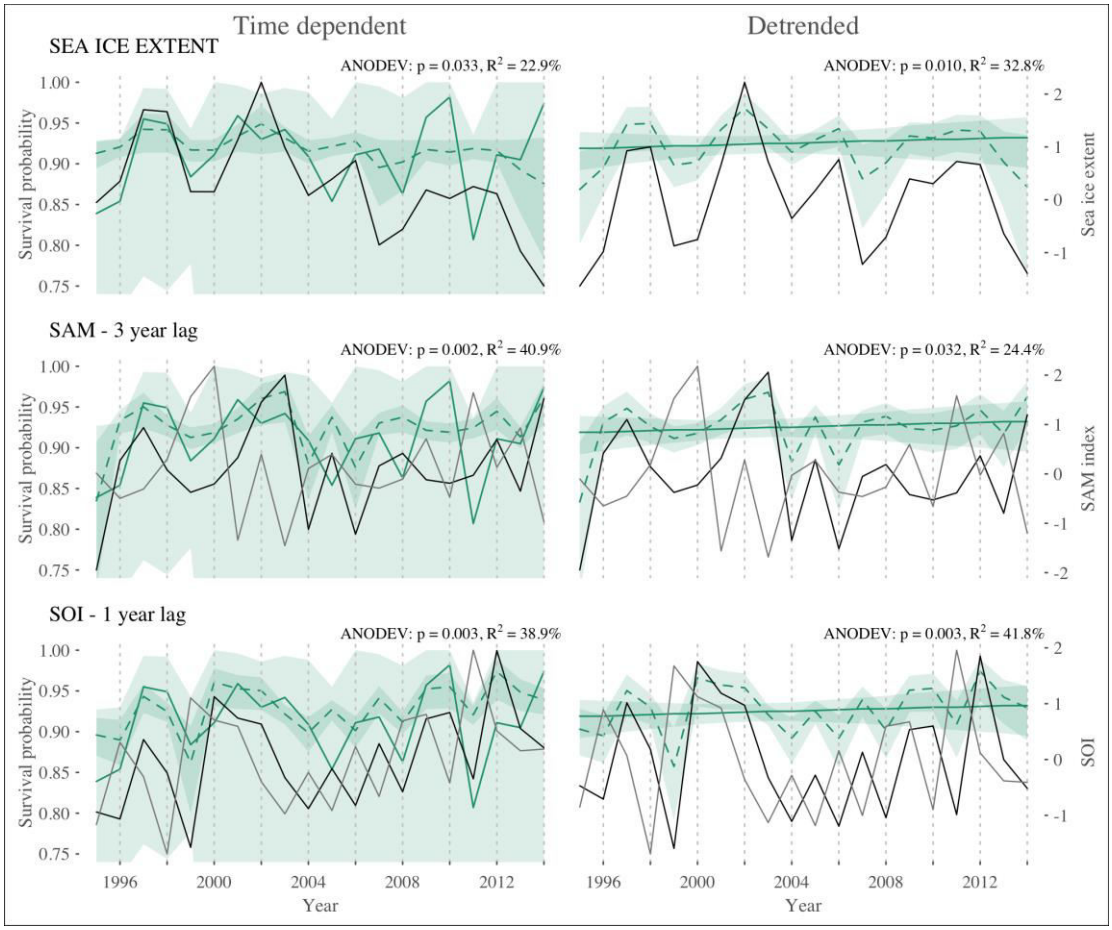

Figure S4 Annual variation in survival probabilities of adult light-mantled albatrosses at Macquarie Island, modelled as time-dependent and linear de-trended (solid coloured lines) and as a function of the covariates (broken coloured lines) including 0.95 confidence intervals with standardised covariates (solid black lines), and temporal lags (solid grey lines).

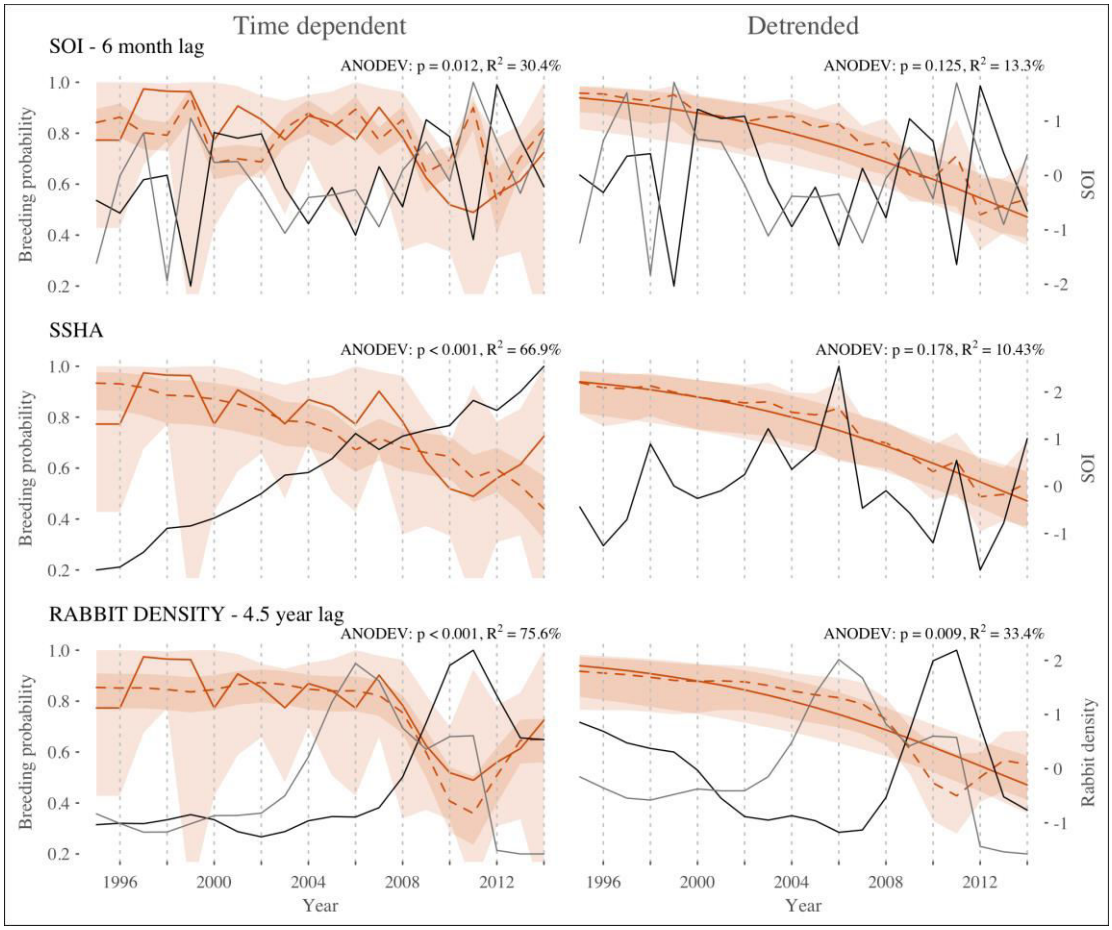

Figure S5 Annual variation in breeding propensity of adult black-browed albatrosses at Macquarie Island, modelled as time-dependent and linear de-trended (solid coloured lines) and as a function of the covariates (broken coloured lines) including 0.95 confidence intervals with standardised covariates (solid black lines), and temporal lags (solid grey lines).

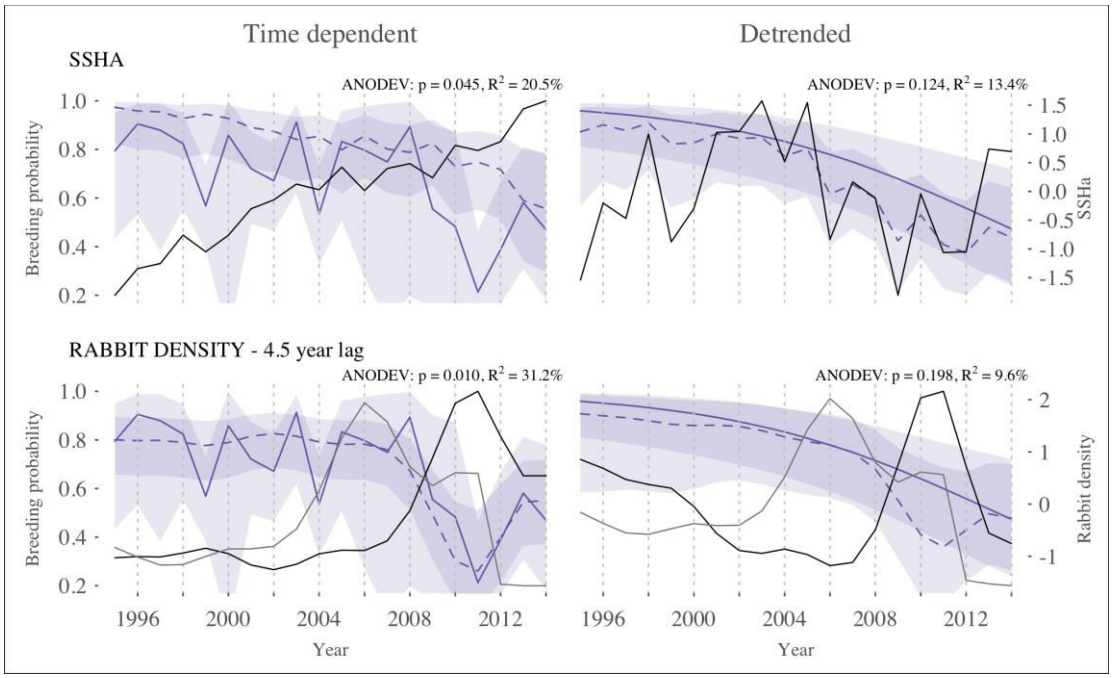

Figure S6 Annual variation in breeding propensity of adult grey-headed albatrosses at Macquarie Island, modelled as time-dependent and linear de-trended (solid coloured lines) and as a function of the covariates (broken coloured lines) including 0.95 confidence intervals with standardised covariates (solid black lines), and temporal lags (solid grey lines).

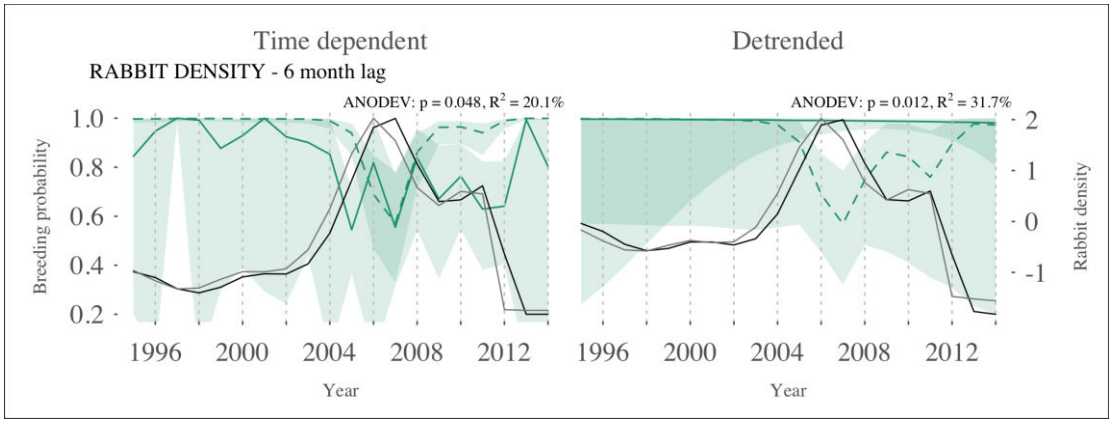

Figure S7 Annual variation in breeding propensity of adult light-mantled albatrosses at Macquarie Island, modelled as time-dependent and linear de-trended (solid coloured lines) and as a function of the covariates (broken coloured lines) including 0.95 confidence intervals with standardised covariates (solid black lines), and temporal lags (solid grey lines).

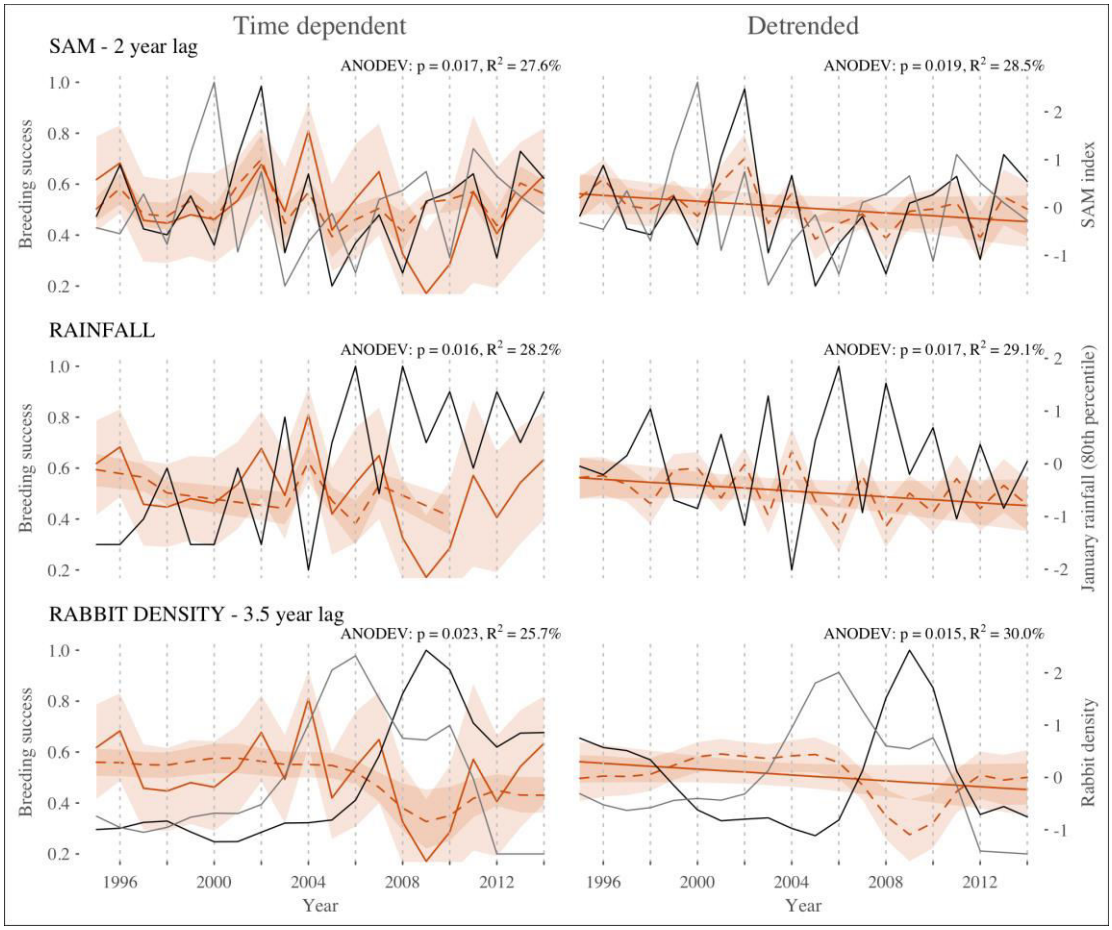

Figure S8 Annual variation in breeding success probabilities of adult black-browed albatrosses at Macquarie Island, modelled as time-dependent and linear de-trended (solid coloured lines) and as a function of the covariates (broken coloured lines) including 0.95 confidence intervals with standardised covariates (solid black lines), and temporal lags (solid grey lines).

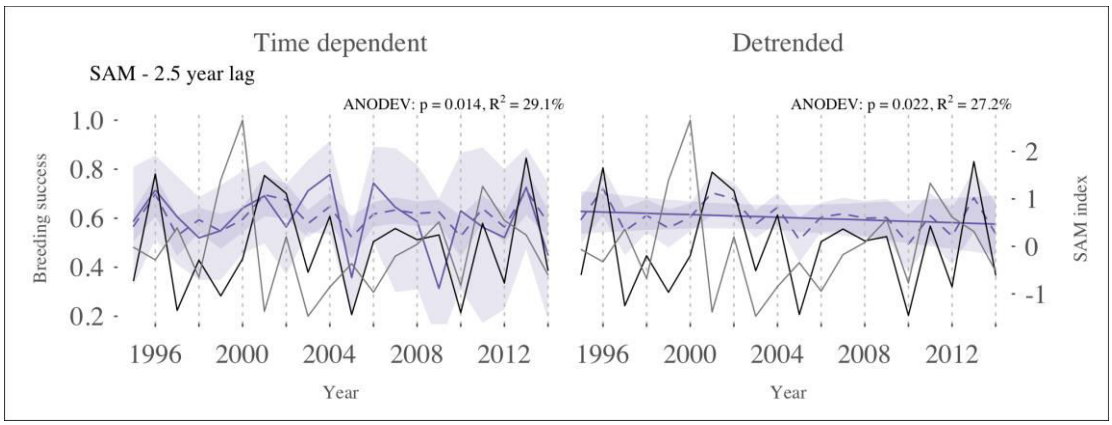

Figure S9 Annual variation in breeding success probabilities of adult grey-headed albatrosses at Macquarie Island, modelled as time-dependent and linear de-trended (solid coloured lines) and as a function of the covariates (broken coloured lines) including 0.95 confidence intervals with standardised covariates (solid black lines), and temporal lags (solid grey lines).

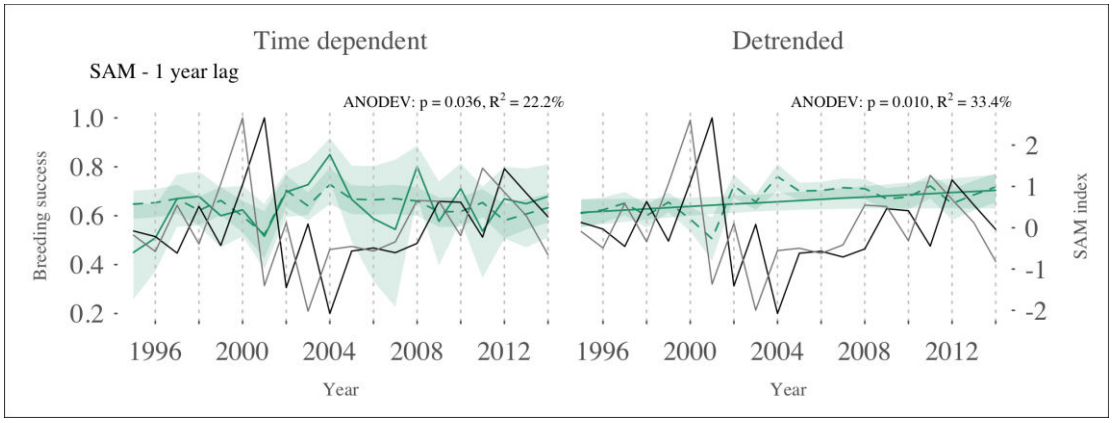

Figure S10 Annual variation in breeding success probabilities of adult light-mantled albatrosses at Macquarie Island, modelled as time-dependent and linear de-trended (solid coloured lines) and as a function of the covariates (broken coloured lines) including 0.95 confidence intervals with standardised covariates (solid black lines), and temporal lags (solid grey lines).

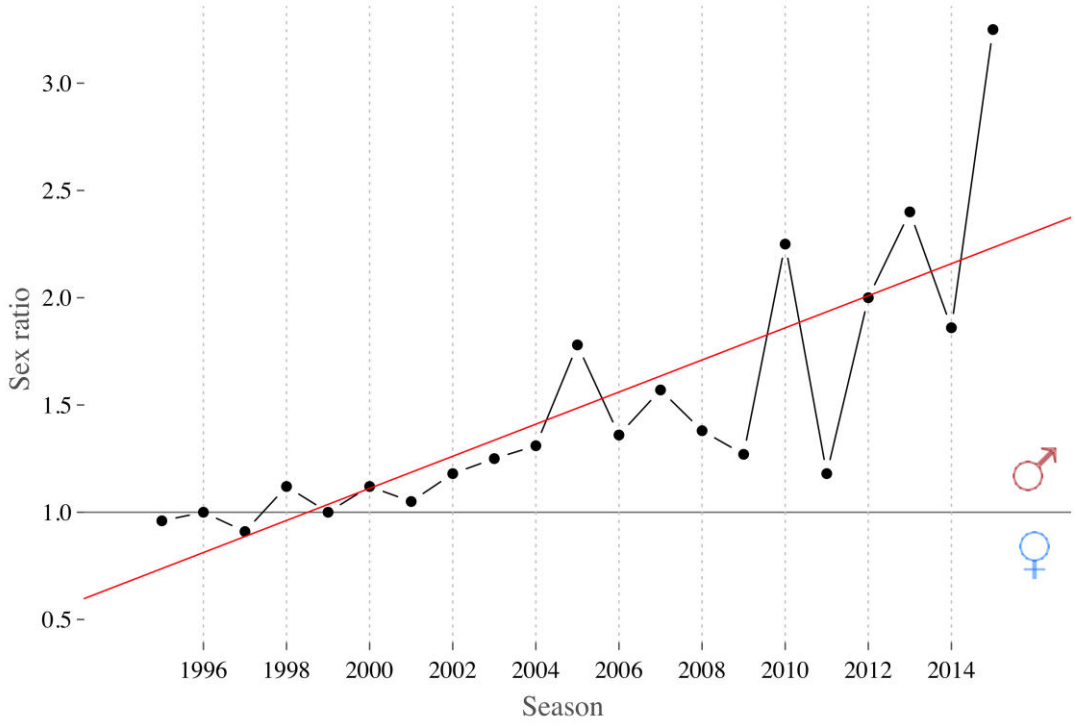

Figure S11 Trend in sex ratio of breeding and nonbreeding wandering albatrosses on Macquarie Island ($F_{1,19}=31.47$, $p<0.001$, $R2=0.60$). Data sourced from DPIPWE (2014).

Chapter 5

General Discussion

In this thesis I aimed to quantify the relationships between albatross vital rates and environmental state to provide a predictive framework for determining how the projected future changes in climate will affect a multi-species community of albatrosses at Macquarie Island. Understanding demographic determinants of wide-ranging pelagic foragers remains a challenge in marine science due to limited knowledge of foraging behaviours (Hays et al., 2016), a shortage of prey information and uncertainty surrounding the relative effects of environmental (e.g. climate) change (Grémillet and Boulinier, 2009) and anthropogenic processes (e.g. fisheries) (Tasker et al., 2000). Studies often rely on proxies and advanced statistical methods to disentangle relationships between demographic and environmental variability (Grosbois et al., 2008). Using a combination of biotelemetry and demographic modelling techniques, this study has produced new information on the ecology of a community of Southern Ocean albatrosses. It has identified core foraging habitats, the indirect influence of an invasive species on reproductive output and estimated the relative contribution of at-sea and onshore ecosystem processes on their vital rates. This discussion will provide an overview and synthesis of the main findings in a broad ecological context, particularly regarding life history theory and population demography with reference to future management decision-making.

Environmental change to population processes

A life history comprises a series of events that occur as an animal ages or transitions through life stages, such as birth, growth, recruitment, reproduction, senescence and mortality (Stearns, 1992). Life histories are shaped under the evolutionary process of natural selection by the interaction between environmental conditions and intrinsic factors that influence genetic variability acting upon individual fitness (Mousseau and Roff, 1987, Stearns, 1992). This adaptation leads to a species adopting particular life history traits that maximize the success of individuals. Individuals adapt to a range of physical conditions across their distribution. It is when environmental conditions exceed the range of conditions to which multiple individuals have adapted that consequences for survival and reproduction can influence a population (Stearns, 2000, Hoffmann and Sgró, 2011). Demographic assessments examine how vital rates, such as age-specific fecundity and survival influence population

processes (Caughley, 1977). By understanding demographic reactions we can determine the strength of selection on life history traits for a range of conditions, representing a critical step in linking population dynamics to environmental influences (Stearns, 1992). Understanding the demographic consequences of environmental variation is becoming exceedingly important due to the increasing and rapid effects of global climate change on ecosystem function (Doney et al., 2012, Constable et al., 2014).

Foraging behaviour

Foraging behaviours provide a link between environmental and demographic variability by influencing the capacity to which energetic resources can be allocated to survival and reproduction (Fig. 1) (Boggs, 1992, Weimerskirch et al., 1997b). Optimal foraging theory predicts that animals will maximise their energy intake per unit foraging time to reduce the risk of starvation and increase the capacity to grow and reproduce (Pyke, 1984). The extent to which foraging efficiency shapes survival and reproduction represents an intrinsic link determined by evolutionary processes between foraging and life history strategies (Boggs, 1992). The foraging behaviour and habitat use of an individual are, therefore, important determinants of resilience or vulnerability to environmental change (Peterson et al., 1998, Paredes et al., 2012).

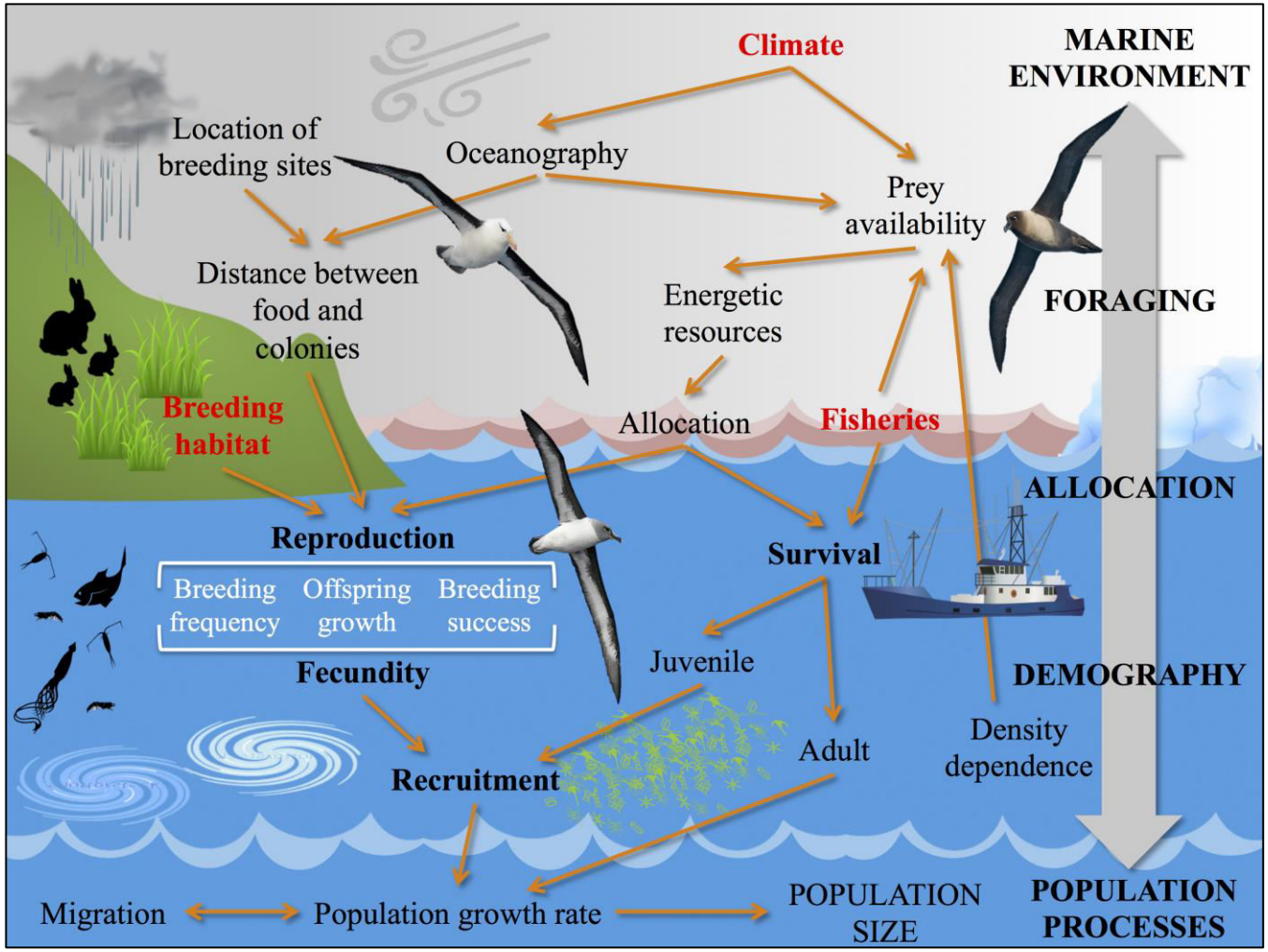

Figure 1 The ecological links (orange arrows) that connect the marine environment to population processes of albatrosses, following the pathway from foraging behaviours, to the allocation of energetic resources and demographic parameters (grey arrow). Adapted from Weimerskirch (2002).

Southern Ocean predators forage in a dynamic marine environment where biological productivity is unevenly distributed and concentrated in regions where oceanographic processes promote nutrient enrichment of surface waters through upwelling and convergence, such as oceanic fronts and eddies (Sullivan et al., 1993, Pakhomov and McQuaid, 1996, Moore and Abbott, 2000). Southern Ocean processes are experiencing major changes due to ocean warming, a result of global climate change, including a southward shift in oceanic frontal systems (Sokolov and Rintoul, 2009), a change in wind patterns (Marshall, 2003) and regional changes in sea ice concentration (Stammerjohn et al., 2012). Changes to oceanographic processes that underpin primary productivity can have pronounced demographic consequences for marine predators by influencing the availability and accessibility of prey resources (Trathan et al., 2012). Changes in the location and availability of prey may influence the energetic cost of foraging and have adverse consequences for species with strong foraging site fidelity such as southern elephant seals *Mirounga leonina* (Bradshaw et al., 2004) less so than species that engage a broad search pattern to maximize prey encounters such as wandering albatrosses *Diomedea exulans* (Weimerskirch et al., 2014). Furthermore, because spatiotemporal data on prey distribution in the Southern Ocean is sparse, knowledge of how predators use water masses and oceanographic features is often used to link environment to foraging behaviours and ultimately population level processes. For African penguins *Spheniscus demersus*, a deeper thermocline resulted in prey being concentrating at greater depths, requiring longer and deeper dives and increased energy expenditure to reach prey (van Eeden et al., 2016). Temporal shifts in prey availability due to environmental factors may also influence population demography by driving ecological mismatches, whereby foraging and reproductive success of predators is dependent on the phenology of prey (Durant et al., 2007). For short-tailed shearwaters *Ardenna tenuirostris* that breed in Tasmania, direct flights to the marginal ice zone off the coast of Antarctica during the early chick-rearing period allow them to exploit the seasonal abundance of Antarctic krill *Euphasia suberba* in this region (Cleeland et al., 2014). If the summer recession of sea ice and subsequent bloom in phytoplankton and krill is delayed, adults may have a diminished capacity to restore body condition and provision chicks. Such relationships highlight the importance of understanding species habitat use and foraging plasticity in response to environmental heterogeneity or changes in the energetic requirements of reproduction.

In Chapter 2, the physical characteristics of core foraging areas of four Southern Ocean albatross species that breed on Macquarie Island provided insight into species resilience to environmental change. Each species within the community possesses unique life history attributes and morphological adaptations that influence their habitat use and capacity to respond to climate-driven changes. Black-browed albatrosses *Thalassarche melanophris*, with a shorter breeding cycle and morphological traits that incur greater flight costs, concentrated foraging more locally during breeding, whereas wandering albatrosses, with a longer breeding cycle and wing morphology adapted to highly efficient flight had a more extensive foraging distribution. The resulting differences in core foraging areas have important implications for susceptibility to environmental change. For example, black-browed albatrosses, with a more northerly distribution, lower flight efficiency and greater reliance on local productivity, may be vulnerable to changes in wind patterns that increase the cost of flight and a southerly shift in the Subantarctic Front (Flynn and Williams, 2012). Despite considerable variation in foraging areas, all species showed similar use of mesoscale eddy features and frontal systems. In a dynamic and variable environment such as the Southern Ocean, these features represent predictable and profitable habitats for marine predators which are reflected in the foraging behaviours of many species, from king penguins *Aptenodytes patagonicus* (Scheffer et al., 2010) to southern elephant seals (Cotté et al., 2015). By investigating the comparative foraging ecology of multiple sympatric species that inhabit different ecological niches this research contributes greater insight into the vulnerability of albatross species to environmental change and provides a broader understanding of ecosystem function.

Demographic responses to ecological change

Studies that quantify the link between foraging ecology and demographic variability in changing environments are at the frontier of marine predator research (Bost et al., 2015). However, for Southern Ocean seabirds that forage across whole ocean basins, relating foraging conditions to variability in demography is complicated by the scale of foraging (Shaffer et al., 2006), the ephemeral nature of the prey field and potential anthropogenic impacts (Jennings and Kaiser, 1998, Lewison et al., 2004, Ryan et al., 2009). Furthermore, long-lived marine predators primarily allocate energetic resources to survival, because the opportunities to reproduce over the course of a lifetime are numerous, allowing them to mitigate the effect of poor foraging conditions in particular years (Dobson and Jouventin, 2010). Additionally, Southern Ocean marine predators exhibit morphological and

physiological adaptations that enable them to buffer survival and reproduction against environmental variability. For albatrosses, morphological and behavioural adaptations that permit highly efficient flight allow them to scour oceans for prey without expending large energetic resources (Pennycuick, 1982, Spear and Ainley, 1997a, Weimerskirch et al., 2000b). Such plasticity is likely to increase fitness and resilience to adverse change in highly heterogeneous and dynamic environments like the Southern Ocean. By assessing variability in multiple demographic rates across multiple species, greater insight into trade-offs between survival and reproduction and the adaptive capacity of individual species to environmental change across their distribution is gained.

Climate change

Large-scale climate cycles drive demographic variability in marine predators due to their widespread influence on ocean processes and subsequently, prey resources (Thompson and Ollason, 2001, Genovart et al., 2013, Bost et al., 2015). Ocean and atmospheric warming associated with global climate change influence climate cycles including the Southern Annular Mode (Arblaster and Meehl, 2006) and El Niño Southern Oscillation (Yeh et al., 2009), corresponding to a southerly contraction and intensification of circumpolar winds and increased strength and duration of equatorial Pacific Ocean warm events, respectively. Climate-driven changes to the physical oceanography and atmospheric processes represent a threat to some marine predator populations through the regulation of prey abundance, distribution and availability (Grémillet and Boulinier, 2009). However, the extent and severity of their impacts are not well understood and options for mitigation not clear.

In Chapter 4, positive Southern Annular Mode indices and La Niña events were associated with increased survival of black-browed, grey-headed *T. chrysostoma* and light-mantled albatrosses *Phoebetria palpebrata*. Furthermore, the survival of black-browed and grey-headed albatrosses was positively associated with more southerly winds and greater wind speeds, respectively. These results represent a direct connection between morphological adaptations and foraging behaviours (Chapter 2), and demographic variability (Chapter 4). With a relatively high wing loading for its size, intensified winds would increase the glide ratios and reduce the energetic cost of flight to grey-headed albatrosses (Pennycuick, 1982, Phillips et al., 2004). Similarly, for black-browed albatrosses, increased southerly winds provide beneficial tailwinds to more northern foraging grounds. The capacity for wind patterns to influence the survival of albatrosses is a relatively new development in the

understanding of procellariiform ecology (Pardo et al., 2017) and suggests that these species are more sensitive to environmental variability than previously credited. Albatrosses are likely to be particularly vulnerable to changes in wind strength, more so than changes in other physical factors, due to the direct influence wind has on the energetic cost of flight (Weimerskirch et al., 2000b, Sachs, 2005). With efficient flight representing the primary adaptation albatrosses have to acquire energy in an environment where prey resources are patchily distributed, the capacity to adapt to changes in wind patterns may be minimal. Furthermore, the consequences of an increasingly positive Southern Annular Mode may be expressed over a latitudinal gradient, with higher latitude foragers such as albatrosses experiencing the positive effects of strengthened winds at high latitudes, including reduced flight costs (Weimerskirch et al., 2012) and increased surface productivity (Daly and Smith, 1993), compared to species that forage across the lower latitudes. Based on the findings of this study, increasingly positive Southern Annular Mode indices and associated strengthened and more southerly winds are likely to have positive implications for the survival of Macquarie Island albatrosses. However, to further understand the affect of wind patterns on survival over the longer-term, a population viability analysis integrating plausible future wind scenarios is required.

Fisheries

Despite comprehensive mitigation policy development, industrial fishing remains a major threat to the survival of Southern Ocean seabirds through bycatch related mortality and resource competition (Tasker et al., 2000, Phillips et al., 2016). Increased mortality from bycatch has significant consequences for seabird population viability as it reduces a core life history trait: longevity. With high adult mortality, the number of viable offspring that can be produced over a lifetime is diminished, and the probability of long-term population viability reduced (Dobson and Jouventin, 2010). For highly migratory albatrosses that forage across multiple fisheries management areas, fisheries risk can be difficult to determine as the relationship between survival and fisheries effort is complicated by substantial spatial heterogeneity in bycatch mitigation and discarding practices (Cox et al., 2007, Gilman, 2011). Furthermore, the relationship between effort and bycatch or discarding rates is dynamic and affected by social, political, economic and ecological factors. Nevertheless, fisheries have been attributed to past catastrophic declines in albatross populations, highlighting the need to prioritise reassessment and resolve uncertainty in the spatial patterns of negative interactions (Gales and Robertson, 1998, Croxall et al., 2012). Furthermore, as

mitigation of regulated fisheries improves (Moreno et al., 2008), innovative solutions are required to limit bycatch in unregulated fisheries and address other harmful ecological drivers of demographic variability to re-establish depleted albatross populations. The combination of multiple and simultaneous stressors can have important consequences for population growth and elasticities. Recent research by Pardo et al. (2017) has shown how bycatch related mortality has driven declines in albatross populations at South Georgia, and that subsequent climate-driven reductions in food availability caused low breeding success that is inhibiting the capacity of populations to recover to past numbers.

For Macquarie Island black-browed albatrosses, fisheries effort in longline operations in the south-west Atlantic, a known overwintering habitat (Chapter 2), explained periodic declines in survival (Chapter 4). The correlation between black-browed albatross survival and fisheries effort complements numerous other studies that have reported high levels of bycatch onboard fishing vessels (Reid and Sullivan, 2004, González-Zevallos and Yorio, 2006, Sullivan et al., 2006, Bugoni et al., 2008) and declines at breeding colonies for this species (Prince et al., 1994). Furthermore, the combination of multiple factors explained anomalously low survival in 2006 including low preceding Southern Annular Mode and Southern Oscillation indices and high fisheries effort in the south-west Atlantic.

These results highlight how multiple stressors that operate across the foraging distribution of a population may have a cumulative impact on demographic processes. However, the effect of multiple stressors on populations is complex, with the potential for combined stressors act synergistically or antagonistically. Quantifying these relationships and their effect is currently beyond the capacity of integrated demographic models and requires further consideration to inform management based conservation actions.

Invasive species

Many seabirds and seals breed on islands that offer habitat for breeding and provisioning young and where few natural predators exist. Changes to island habitat quality can have consequences for the demographic variability of predominantly marine species. These primarily include changes that influence the energetic cost of survival (Cummings et al., 2015) or reproduction (Brothers and Bone, 2008), predation rate (Horswill et al., 2014) or competition for breeding habitat (Sullivan and Wilson, 2001). Native species may be affected in these ways by the presence of invasive species, which can rapidly transform island

ecosystems (Selkirk et al., 1983, Scott and Kirkpatrick, 2008). For seabirds, invasive mammals are particularly problematic as they can directly depredate individuals or compete for nesting habitat, subsequently having a detrimental effect on seabird vital rates (Van Aarde and Skinner, 1981, Brothers, 1984). For instance, invasive mice *Mus musculus* populations on Gough Island in the South Atlantic Ocean depredate live Tristan albatross *Diomedea dabbenena* and Atlantic petrel *Pterodroma incerta* chicks, reducing breeding success to exceptionally low levels (Cuthbert and Hilton, 2004). In the case of Macquarie Island, competition for burrows by invasive rabbits *Oryctolagus cuniculus* has been identified as the cause of low burrow occupancy of several burrowing petrel and shearwater species, which is likely to have had negative consequences for overall reproductive output (Brothers, 1984, Brothers and Bone, 2008). Cases of predation and competition for breeding sites are well documented in the literature (Brothers, 1984, Huyser et al., 2000, Jones et al., 2008, Hilton and Cuthbert, 2010). However, less well understood are the indirect and cascading consequences of invasive mammals on seabird survival and reproduction. In Chapter 3, I report the indirect relationship between high rabbit density and the reproductive output of three albatross species, whereby reductions in breeding propensity are linked to severe habitat degradation of albatross nesting sites caused by heavy rabbit grazing. For black-browed albatrosses, the combination of high rabbit density and heavy rainfall events was also linked to lower breeding success. The combination of both stressors may have had a synergistic effect on breeding success, whereby high rabbit density suppressed vegetation vital for shelter during heavy rainfall events and strengthened the effect on black-browed albatross chicks. The influence of a non-predatory invasive mammal on the reproductive capacity of multiple ground-nesting seabird species is a unique finding, particularly given that research on the underlying processes that determine breeding propensity are mainly focused on factors such as breeding experience, adult quality and at-sea conditions (Barbraud and Weimerskirch, 2005, Lee et al., 2007). These results show how the cumulative effect of climate-driven extreme weather and invasive species can negatively influence the demography of multiple native species.

Population-level responses

The life history traits of individuals contribute to the resilience of their populations to environmental variability. For albatrosses, their long life, high adult survival and low fecundity make their populations vulnerable to increases in adult mortality and resistant to periodic reductions in reproductive output (Weimerskirch et al., 1987). This hinges on being

able to produce few high-quality offspring over the course of a lifetime, representing low fecundity and contributing to a low intrinsic rate of increase (Stearns, 1992). For the population to subsist, only few young are required to recruit back into the population. The Macquarie Island albatross populations have differing long-term trends; two species are increasing (black-browed and light-mantled albatrosses), one decreasing (wandering albatrosses) and one has a stable population trajectory (grey-headed albatrosses). In Chapter 4, I found no indication of an increase in adult survival, breeding propensity or breeding success for either black-browed or light-mantled albatrosses, suggesting that further investigation into juvenile survival and recruitment is required to disentangle population trends. In contrast, negative trends in adult survival and breeding propensity were detected for wandering albatrosses, contributing to the observed population decline.

It is important to note that indications that the boundaries of several light-mantled albatross study sites have contracted over time exist (DPIPWE, 2014), leading to some individuals being encountered on the first occasion and not encountered on subsequent occasions. This may dampen any positive trend in survival, if not accounted for by tests for transience. Similarly, observed declines in breeding propensity are not corroborated by annual counts of breeding pairs. This may be explained by periodic reductions in detection probability for grey-headed and black-browed albatrosses due to poor slope condition leading to increased uncertainty surrounding counts of breeding pairs. These limitations highlight the challenges associated with the long-term monitoring of secretive species and the importance of capturing trends in demographic rates to infer population level change.

Implications for conservation

This study has quantified the relative influence of multiple factors to survival and reproduction, offering the opportunity to consider dynamic management strategies. For highly migratory marine species, which forage across whole ocean basins, traditional conservation strategies such as marine protected areas that have fixed boundaries may be ineffective (Bull et al., 2013). Conservation offsetting represents a dynamic management strategy, whereby one or multiple threats are offset through mitigation of others so as to achieve no net loss, in this case, in population growth (Gardner et al., 2013). The control or eradication of predatory invasive species may adequately offset fisheries bycatch mortality of seabirds (Wilcox and Donlan, 2007). On Macquarie Island, severe habitat degradation caused by invasive rabbit populations is linked to substantial declines in reproductive output of

multiple albatross species (Chapter 3) and represents an unanticipated consequence of reduced rabbit control leading up to the eradication in 2010 (Springer, 2016). For black-browed albatrosses, which exhibited lower survival in relation to high fisheries effort in the south-west Atlantic (Chapter 4), the eradication of rabbits (Springer, 2016) and subsequent vegetation recovery (Shaw et al., 2011) is expected to result in improved breeding propensity and success. This may offer some benefits to population growth through increased future juvenile recruitment. However, the life history of albatrosses makes their populations more sensitive to increased adult mortality but resistant to periodic reductions in reproductive output. It therefore seems unlikely that the removal of rabbits would provide compensatory mitigation of fisheries bycatch. Furthermore, this scenario represents a conservation strategy that fails to meet the criteria for effective compensatory mitigation for marine bycatch (Finkelstein et al., 2008). Perhaps more importantly, this research offers findings that allow for informed identification of viable management options and reduced outcome uncertainty of conservation actions within existing frameworks such as the Agreement on the Conservation of Albatrosses and Petrels and Commission for the Conservation of Antarctic Marine Living Resources. By addressing three major threats that operate across three different scales of manageability: local on island ecosystem shifts, distant and dynamic fisheries and broad scale oceanic variability, this research provides insight into the value of alleviating pressures that are more logistically or politically manageable. Changes to oceanic processes represent a threat for which management strategies are less obvious. For Macquarie Island albatross populations, large-scale climate cycles, sea ice variability, wind patterns and extreme rainfall events explained significant demographic variability. With current and predicted future climate change driven changes to onshore and oceanic processes conservation managers may be forced to consider more radical options for managing these populations. Innovative solutions such as shelters to protect chicks from heavy rainfall and storm events and supplementary feeding of pre-fledglings that improve breeding success and juvenile recruitment rates may become vital strategies for preventing future population declines. Artificial shelters that protect nesting seabirds from adverse weather are already known to be effective and have been observed to reduce the energetic cost of incubation of Artic breeding common eiders *Somateria mollissima* by reducing exposure to strong winds (Høyvik Hilde et al., 2016).

This research also indicates where the greatest uncertainty lies and more research is required to inform conservation efforts. Grey-headed albatrosses breeding on Macquarie Island are

predominantly biennial, however, a small portion of the population attempt to breed annually, similarly to Marion Island conspecifics (Ryan et al., 2007). These individual life history traits increase the uncertainty in modelled demographic parameters and environmental relationships detected for the small population. Improving detection probability and exploring age- and sex- related demographic models might further resolve uncertainty associated with this species. Uncertainty in estimates is an inevitable consequence when modelling small populations. However, understanding the external drivers of demographic variability is critical to assess population viability, particularly in small populations where minor decreases in vital rates can have a considerable impact on the population. By investigating contrasting and corresponding responses of related sympatric species to common environmental conditions provides greater insight into specific ecological relationships and adaptive capacity of each species. No synchronicity in demographic variability was detected in the Macquarie Island albatross community, suggesting that unique life history and foraging ecology results in differing resilience to ecological change (Chapter 4). However, commonalities existed, with broad-scale climate cycles and habitat degradation affecting survival and reproductive output of three species.

Science communication

Funding for conservation management and scientific research often hinges on what is perceived to be important to the public in a political context (Martín-López et al., 2009). There is a strong imperative to engage with the public to communicate research findings and advocate for policy implementation (Bielak et al., 2008). Research on Southern Ocean marine predator species offers itself as an obvious platform for effective communication through the stories of iconic wildlife, extreme behaviours and captivating imagery (Davis, 2007). Biotelemetry presents further avenues for science communication as it facilitates engagement with a broad audience through multidisciplinary links across the fields of science, technology, engineering and mathematics. Furthermore, communicating the journeys of individual animals allows interested people to investigate and discover unknown environments from the animal's perspective through narrative, such as elephant seal foraging in the deep ocean. The journeys of individual animals that explore dynamic and changing environments offer scientists a point of transition to broader ecological concepts, including population ecology, ocean processes and global climate change. However, for researchers science communication initiatives are often voluntary and do not contribute directly to scientific outputs. For both scientists and the public to move beyond altruism and support

each other to move forward academically and politically, science communication initiatives require a feedback framework whereby specific outcomes that support both groups can be achieved and ideally lead to improved scientific and conservation efforts (Appendix 2).

Perspectives

By using species distribution and demographic modelling approaches this study has provided a quantitative understanding of the mechanisms linking climate to demographic change and served as a basis for predicting the responses to future climate-driven change for a community of Southern Ocean albatross species. The analysis of community habitat use has supported knowledge that foraging behaviours are intrinsically linked to the life history and morphological constraints of each species and that albatrosses concentrate effort on oceanographic features that aggregate prey resources. This study has quantified indirect links between invasive rabbits and reduced reproductive output of an albatross community, suggesting that the recent eradication of invasive vertebrates will have positive benefits for the Macquarie Island populations. Lastly, by assessing the influence of fisheries, oceanic and onshore threatening processes on multiple demographic rates of several sympatric albatross species, this study has highlighted the need for conservation management strategies to address each species separately, based on their unique life history traits, demography and foraging ecology. These findings illustrate the importance of multiple onshore and at-sea threat types when assessing demographic variability and the development of management policy. This study provides support for evidence-based conservation planning for these populations as well as reducing outcome uncertainty of future management actions for other marine predator populations. Furthermore, this study has provided new insights into the ecology of a community of Southern Ocean predators and has broader applications for understanding the responses of multiple sympatric species to multiple environmental threats.

Appendix 1.

Resolving data discrepancies in the Macquarie Island Albatross and Giant Petrel Database

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The Macquarie Island Albatross and Giant Petrel Database

Data from the Macquarie Island Albatross and Giant Petrel monitoring program is contained in a relational Microsoft Access database under the custodianship of the Marine Conservation Branch, Department of Primary Industries, Parks, Water and Environment, Tasmania. It is also archived with the Australian Antarctic Division Data Centre. The database encompasses mark-recapture data from four albatross (black-browed, grey-headed, light-mantled and wandering albatross) and two giant petrel (northern and southern giant petrel) species from as early as 1952. The database is divided into five linked tables that broadly cover individual bird (sex and species), resight (resight state), banding (metal and plastic) and breeding (partnerships, offspring and breeding outcomes) data. Tables are linked through two different unique numeric identifiers, *Bird_ID* and *Resight_ID*, whereby each bird banded and each bird resight has a unique identifier (Fig. 1).

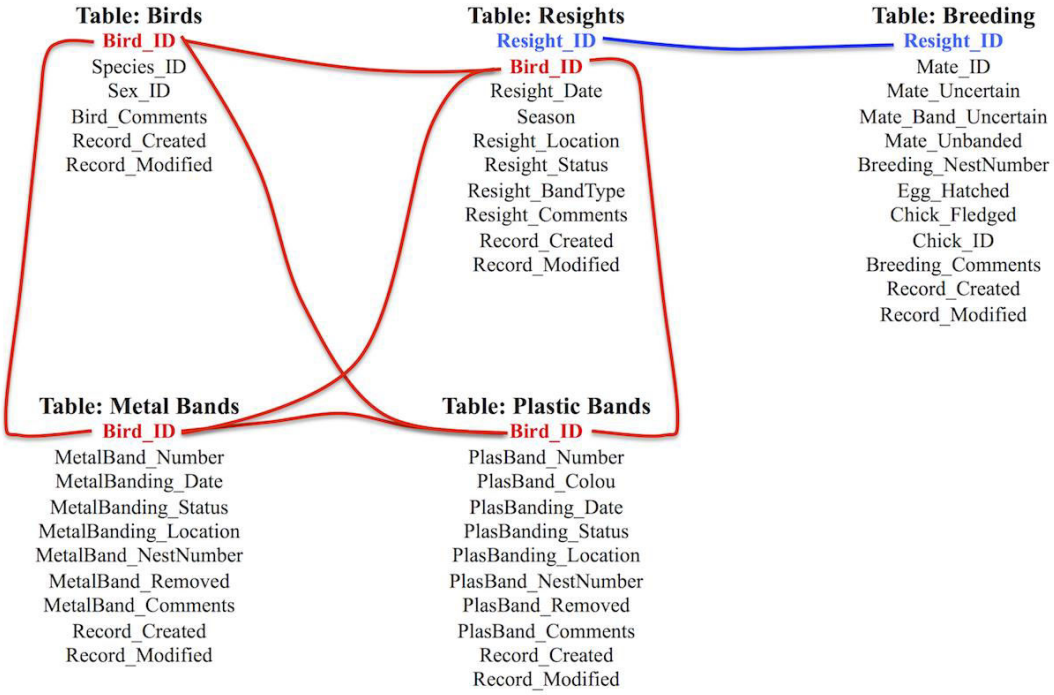

Figure 1 Relationships between data tables and associated fields in the Macquarie Island Albatross and Giant Petrel Database linked by the primary keys *Bird_ID* and *Resight_ID*. *Mate_ID* and *Chick_ID* values are also used to identify individual birds (matching the *Bird_ID* key), however these are not linked.

Data inconsistencies and handling

Initial inspection of the database for this PhD project identified substantial data discrepancies and created a framework to resolve these. The original data were contained in a series of Microsoft Excel worksheets that were periodically imported into the Access database. However, for some species, the archived worksheets did not cover the full temporal range of the monitoring program (i.e. the full data record was not available in the worksheets, only the database). Furthermore, substantial inconsistencies existed between the extent of annual records between the database and the original worksheets. From the beginning of the development of the database through to April 2014, snapshots containing the latest data were periodically saved, with each filename containing the corresponding timestamp.

Anecdotal evidence, data exploration and cross-checks were used to identify the origin of the data discrepancies. In June 2010, a Microsoft Access software upgrade resulted in an update to *Bird_ID*, but not *Resight_ID*. Each individual bird has a unique *Bird_ID* value. These values are also referenced in the *Chick_ID* and *Mate_ID* entries in the breeding table. However, *Chick_ID* and *Mate_ID* did not have a formal relational link in the database. During the update, *Bird_ID* values were changed (the existing non-contiguous sequence of

Bird_ID values was replaced with a contiguous sequence) but neither *Chick_ID* nor *Mate_ID* values were updated to match the new *Bird_ID* values. In November 2010, the *Resight_ID* was also updated.

As data entry relied on being able to accurately identify the correct *Bird_ID* corresponding to a band number observed in the field, errors permeated through subsequent versions of the database. There is some evidence that the incorrect *Chick_ID* and *Mate_ID* were used to identify *Bird_ID* corresponding to a band number and vice versa, resulting in cascading errors.

Data recovery options

Reverting to the last version of the database before the June 2010 update and re-entering data from 2010 was considered, but deemed unsuitable because the archive of worksheets was incomplete, and also because errors that had been corrected directly in the database were not documented (and so could not easily be re-corrected after re-entry of data). Furthermore, several discrepancies between snapshot filename timestamps and the actual last modification date of each snapshot file created ambiguity about surrounding the sequence of data entry.

Instead, a data repair procedure was conducted in order to correct the errors in the database. This option was also favoured by the fact that the majority of the inconsistencies in the database were a result of the identifier mismatches, and were therefore relatively systematic and predictable in nature and thus amenable to post-hoc correction.

Data recovery

All data quality control tasks were performed using R and contributed packages (*RODBC* and *sqldf*) and collated into a document for future reference (Ripley and Lapsley, 2014, Grothendieck, 2014, R Core Team, 2016).

1. Each version of the database was compared to each other version to establish the sequence of data entry. Differences between the previous and current database were extracted and assessed after the chronology of data imports was identified. Band numbers were used to cross-reference *Bird_IDs* from a master list, extracted from the database preceding the update. Old and new *Bird_IDs* that did not match were

updated according to the master list. A series of cross checks were implemented to ensure that *Bird_IDs*, *Mate_IDs* and *Chick_IDs* were consistent across tables.

2. Banding, breeding and resight data from all accessible worksheets from 1994 to 2014 were compiled into a complete master file. As the worksheets represent the most reliable form of data available, these entries were then entered into the database, overwriting only previous incomplete or conflicted entries. Where entries were incomplete in the worksheets, the database entries were assessed and either retained or discarded. This step had the greatest effect on the breeding table and updated almost all ~10,000 entries.

3. Data within tables was standardised and formatted for consistency. A cross-referencing exercise allowed for missing or incomplete entries to be updated across all tables. For example, if *Chick_ID* was present, then the corresponding *Egg_Hatched* and *Chick_Fledged* entries were updated. Similarly, if a banding entry did not have a corresponding resight entry, one was created. As the research contained in this thesis required accurate multi-state encounter histories, each *Resight_Status* was cross-referenced for every resight. For example, if a breeding entry indicated that the egg hatched, but the chick did not fledge, the state would be updated to failed breeder chick stage (F. BRc). A set of rules was formulated to ensure such changes were made consistently across tables.

4. Several automated functions were also developed to assist data recovery that achieve the following:
    - Identify data gaps by assessing data entry patterns.
    - Identify potential errors by assessing patterns in breeding frequency and re-mating rates.
    - Establish potential band numbers when a single or multiple digits are missing.
    - Identifying mismatches in data based on biological constraints e.g. interspecies breeding.

5. Following the data quality control, all tables were exported into a new version of the Microsoft Access Macquarie Island Albatross and Giant Petrel Database. Details of

the data processing and associated scripts are contained within a single document that outlines each step taken to ensure data accuracy and the code to reproduce those steps. This document, along with all the database versions assessed, processing scripts and the final database are housed together in a data repository in the Australian Antarctic Data Centre. Data repair in total took ten person-months of full time work by the lead author and three person-weeks of full time work by the co-author. The sheer size of the reference document (130 pages) means it is impractical to include in this thesis, despite representing a considerable contribution to it.

Future directions

The repair procedure described above was sufficient to bring the Macquarie Island Albatross and Giant Petrel database to a mostly-correct state, suitable for use in this thesis. However, despite the extensive work done to rectify the data, some minor errors have persisted. Errors remaining in the current version of the database stem from previous ad-hoc fixes of a small number of records rather than a thorough systematic and automated process. These minor fixes were not applied consistently across the database as a whole making them both difficult to identify and hard to rectify. For instance, *Mate_ID* and *Chick_ID* were corrected for a portion of wandering albatross records, however not for the remaining species, and such changes were not saved to a new version of the database, but saved with previous data imports. In this case, records had to be manually assessed and corrected as most pertained to records from before 1994 and worksheets were inaccessible. Errors remaining in the current version of the database were excluded from analysis contained within this thesis. To maximise the capacity of the database and increase consistency across tables further formatting of character data fields such as *PlasBand_Colour* and *Resight_Location* could be undertaken. This could involve removing typographical errors and establishing a set of discrete factors for each character data field. Furthermore, resight locations could be spatially referenced, and for wandering albatross, photo data could be integrated into individual resight entries.

Appendix 2.

Geolocation Journeys: a Science+Arts collaboration supporting marine predator research.

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Geolocation Journeys is an innovative collaboration between marine predator scientists at the Institute for Marine and Antarctic Studies and artists from the Tasmanian College of the Arts helping to increase public awareness and support Southern Ocean marine predator research.

Geolocators are tracking devices used on Southern Ocean marine predators, from delicate shearwaters to imposing elephant seals. Geolocators record ambient light levels, water temperature and time, enabling scientists to determine location and uncover the foraging movements of predators to identify regions of high ecological significance. Using similar techniques to early mariners, scientists determine an animal's location from recorded light levels, with the length of daylight unique to a given latitude, and the time of noon is specific to a given longitude. An understanding of how marine predators use their ocean habitats, and in particular how these regions are affected by human activities such as industrial fishing and climate change, can enable more effective management strategies to be put in place for their protection.

Geolocation Journeys brings together scientists and artists to create unique wearable artworks using 'retired' geolocators, to raise awareness of the extreme migrations these species embark on and the changing climate they are currently experiencing. By sharing artworks with the non-scientific community through public talks, school workshops and open days these tactile objects metaphorically transport people into the Southern Ocean, with a view from the perspective of a seabird or seal. Through donations, the public can continue the journey of the geolocator as wearable art, and support the purchase of new geolocators for future of marine predator research. These tiny pieces stimulate and aid critical dialogue about the Southern

Ocean and the rapid changes it is experiencing. This project appeals to a broad, curious audience and captivates those ecologically minded by bridging the fields of art, ecology, physics, astronomy, engineering and mathematics.

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